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## Important Features of the Dromaeosaurid Skeleton II: Information from Newly Collected Specimens of *Velociraptor mongoliensis*

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### ABSTRACT

The postcranial anatomy of several new specimens of *Velociraptor mongoliensis* is described. This description concentrates on poorly known aspects of the skeleton of *Velociraptor mongoliensis*, including several features that are extremely similar to characters found in basal avialans like *Archaeopteryx lithographica*. Among these the pelvis and shoulder girdle display several characters such as a reduced antiliac shelf, a furcula, a scapula lying in a subhorizontal position relative to the dorsal column, and sternal plates that articulate with the coracoids. Some problematic features and conditions such as the hypopubic cup and the degree of opisthopubis are also discussed in relation to claims made about these features in regard to the origin of Avialae. Comparisons are made between *Velociraptor mongoliensis* and the enigmatic maniraptoran *Unenlagia comahuensis*.

### INTRODUCTION

In a recent paper (Norell and Makovicky, 1997) we described selected features of the dromaeosaurid skeleton based on new material collected during the Mongolian Academy of Sciences–American Museum of Natural History Expeditions to the Gobi Desert (Novacek et al., 1994, Novacek, 1996). Here

we expand that description to additional velociraptorine dromaeosaurid specimens, keying on poorly understood details of dromaeosaurid anatomy. Descriptions here are based primarily on three specimens: a partial skeleton of *Velociraptor mongoliensis* collected at Tugrugeen Shireh in 1991 (IGM 100/976), a second specimen collected at the nearby locality of Chimney Buttes in 1993 (IGM

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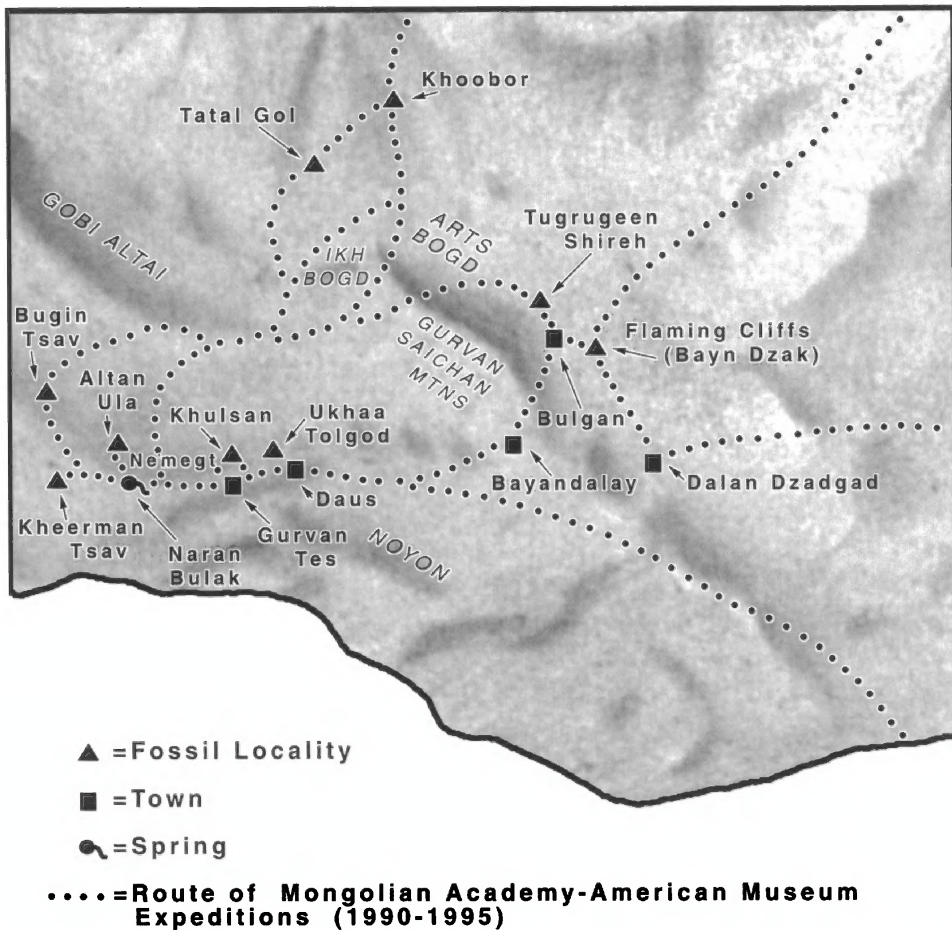


Fig. 1. Map of the south Central Gobi showing Tugrugeen Shireh, Bayn Dzak, and adjacent localities. Chimney Buttes lies 2 km northeast of Bulgan.

100/986) (fig. 1), and a third (IGM 100/982) collected at the Flaming Cliffs (Bayn Dzak) in 1995. Although aspects of the anatomy of some of these specimens have been referred to previously (Norell et al., 1992, 1997; Norell and Makovicky, 1997), these well-preserved specimens require additional attention and illustration, especially in light of inaccurate claims concerning dromaeosaurid anatomy in discussions of avialan origins (Ruben et al., 1997; Feduccia and Martin, 1998).

Major contributions to our knowledge of postcranial anatomy of *Velociraptor mongoliensis* have been made by Barsbold (Barsbold, 1979, 1983). Ostrom's work on specimens of *Deinonychus anthiropus* (Ostrom, 1969a, b, 1974, 1976b, 1990) is noteworthy

both for its completeness and its phylogenetic implications. This paper is seen as a supplement to these important studies.

Published work on the theropod collections made during the AMNH-MAS expeditions is beginning to appear, and several of these specimens are referred to in other publications. To avoid ambiguity, and to clarify information such as collection dates and localities, an annotated list of those specimens that have been referred to in our publications is provided in appendix 1.

Currently there is considerable confusion in the literature regarding usage of the terms bird, Aves, avian, Avialae, and avialan (see discussion in Gauthier, 1986; Norell et al., 1993; Patterson, 1993a, b). Here we use the term Avialae to represent all of the descen-

dants of the last common ancestor of *Archaeopteryx* and living Aves. The term Aves is used for the living diversity as originally proposed by von Linné (1758), which can be cast in an evolutionary context as all of the descendants of the last common ancestor of all living avialans. Because it has no precise definition, the vernacular collective term "bird" is not used except parenthetically.

#### MATERIAL

IGM 100/976 is a partial skeleton found in situ in 1991 (figs. 2, 3, 5, 6). It includes a fragmentary skull and partial postcranium. This postcranium is limited to a few cervical vertebrae, an articulated, but slightly distorted pectoral girdle, and the proximal forelimbs. The specimen was collected over two field seasons. It was referred to *Velociraptor mongoliensis* by Norell et al. (1993) based on comparison of cranial material with the holotype (AMNH 6515). Photographs of this specimen in the ground have been published by Dingus and Norell (1996).

IGM 100/986 is a partial skeleton found in situ with various postcranial and cranial fragments collected as float (figs. 4, 10–17, 20–22). Postcranial elements preserved include an articulated tail, left and right feet and hindlimbs, an articulated pelvis with adjacent cervical and thoracic vertebrae, a scapulacoracoid, and fragmentary forelimb elements.

Because this locality has not been previously reported in the literature it deserves special mention here. Chimney Buttes was found during the 1993 field season as we traversed the open country between Bulgan and Tugrugen Shireh (fig. 1). Lithologically, the locality is composed of bright red structureless sandstones (see Loope and Dingus, 1998) similar to the Flaming Cliffs at Bayn Dzak and very unlike the white aeolian sands of Tugrugen Shireh, which lie in closer proximity (see Fastovsky et al., 1997). Preliminary assessment indicates that Chimney Buttes lies stratigraphically between the younger sediments of Tugrugen Shireh and the older rocks of Bayn Dzak (the Flaming Cliffs). All three localities are considered part of the Djadoktha Formation. Remains of several dinosaurs including ankylosaurs and

both juvenile and adult *Protoceratops andrewsi* were found at the Chimney Buttes locality along with the remains of mammals, lizards, and dinosaur eggs. IGM 100/986 is referred to *Velociraptor mongoliensis* based on comparisons of cranial material with the holotype (AMNH 6515).

An additional specimen of *Velociraptor mongoliensis* (IGM 100/982) (figs. 7, 8, 26) was collected in situ at the Flaming Cliffs during the 1995 expedition near the Volcano sublocality. This specimen is represented by a well-preserved skull and torso with limbs, missing only the distal part of the tail. The ends of long bones as well as many small elements are either missing or severely fragmented, apparently the result of scavenging. Nevertheless the specimen is preserved in near perfect articulation. It is referred to *Velociraptor mongoliensis* based on comparisons of cranial material with the holotype (AMNH 6515).

In our previous paper we referred another specimen, IGM 100/985, to the Dromaeosauridae without more specific reference. This was because of a lack of cranial material allowing comparison with the holotype. The additional specimens described here, which do include cranial material, allow us to refer IGM 100/985 to *Velociraptor mongoliensis*, as all of the corresponding elements present in this specimen are within the range of variation seen in IGM 100/986, IGM 100/976, and IGM 100/982.

Comparisons are made with additional material from Khulson (IGM 100/980 and IGM 100/981). It can be referred to the Dromaeosauridae on the basis of pedal and tail morphology, but insufficient elements are present to refer these specimens to *Velociraptor mongoliensis*.

This collection of specimens, which to our knowledge represents the largest assemblage of articulated dromaeosaurid postcrania yet described, preserves many parts of the dromaeosaurid skeleton that have heretofore been poorly described or unknown. Paramount among these, and the areas of the skeleton that we will consider are: the hind limb, the pelvis and sacrum, the tail, the posterior dorsal and cervical vertebrae, the pectoral girdle, and the manus.



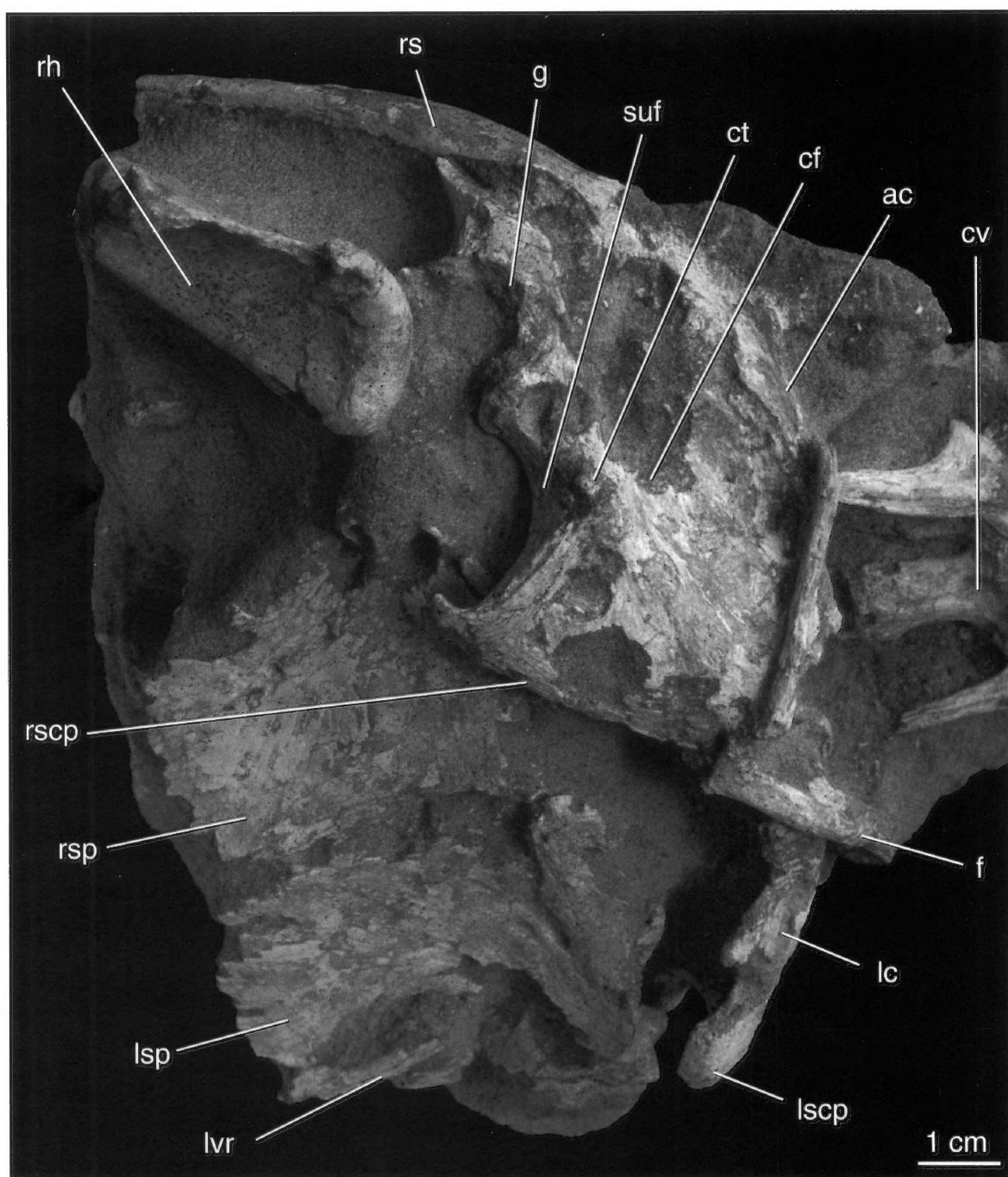


Fig. 2. IGM 100/976. The anterior thoracic region of *Velociraptor mongoliensis* in oblique right ventral view. Labels are spelled out in appendix 2.

## DESCRIPTION

### THE PECTORAL GIRDLE

Aspects of the pectoral girdle (with emphasis on the furcula) of IGM 100/976 were

discussed in a preliminary paper by Norell et al. (1997). The pectoral girdle of dromaeosaurids was also considered in Ostrom (1969a, 1974, 1976a) and Norell and Makovicky (1997). The pectoral girdle of IGM

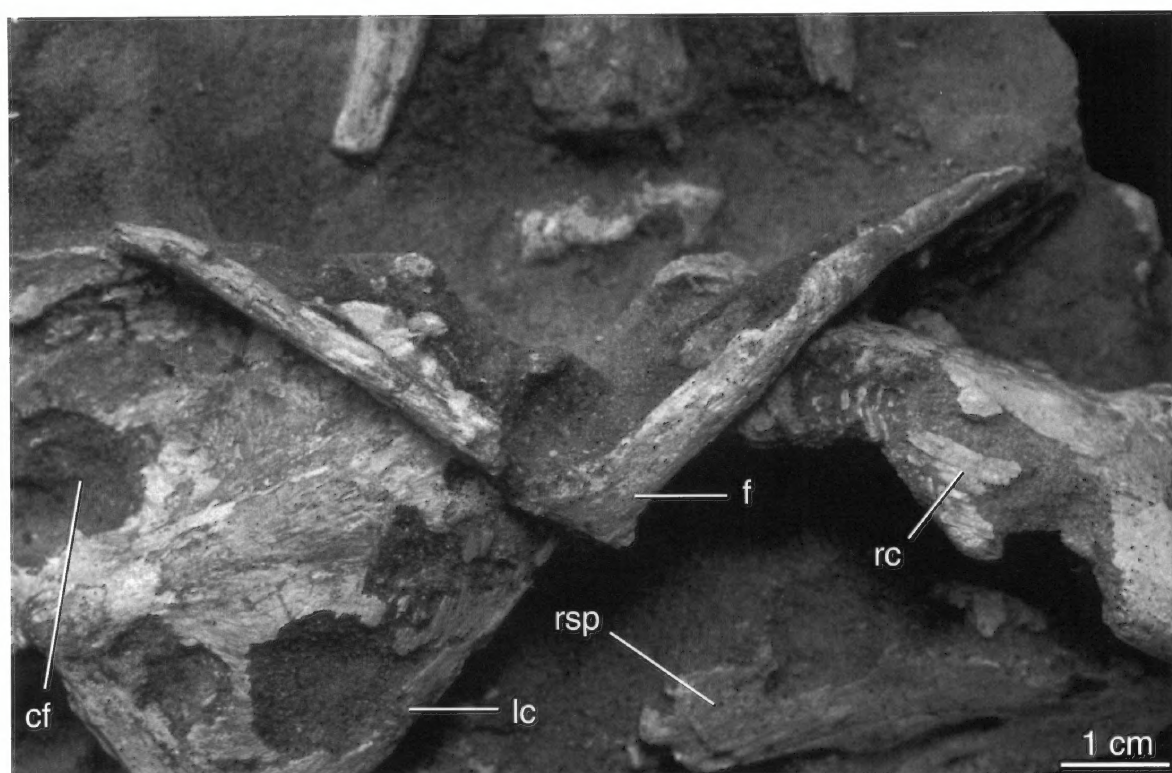


Fig. 3. Furcula of IGM 100/976. Labels are spelled out in appendix 2.

100/976 is preserved in articulation and is composed of the scapulocoracoids, the furcula, and the sternal plates (figs. 2, 3). IGM 100/982 preserves the pectoral girdle in articulation; however, many of the elements are damaged (fig. 7). The skeleton of IGM 100/986 preserves only parts of the left scapulocoracoid and sternal plate (fig. 4).

The sternal plates in IGM 100/976 (fig. 2) are nearly identical to those described by Norrell and Makovicky (1997) in IGM 100/985. However, one notable feature not preserved in the latter specimen, but apparent on IGM 100/976, is the articulation of three ossified sternal ribs with the left sternal plate (fig. 5) as in oviraptorids (Clark et al., 1999). None of the specimens preserves the lateral margin of the sternum, which would indicate the presence of articular facets for these elements. The width of the ventral edge of the coracoid corresponds well with the width of the articulation for the coracoid on the anterior edge of the sternal plate (fig. 2). In IGM 100/986, a small fragment of the sternal plate was found in articulation with the ven-

tral margin of the coracoid. In IGM 100/982, the sternal plates are extremely poorly preserved (fig. 7); however, it can be determined that they consist of articulated paired elements lying in the same position as in IGM 100/976 and IGM 100/985.

The scapulocoracoids are poorly preserved on all specimens, yet several features that have not been previously described are apparent. The scapular blade is narrow and straplike (figs. 4, 6). In lateral view, the scapular blade widens slightly distal to the glenoid. In dorsal view the scapular blade thins distal to the glenoid. The entire scapulocoracoid is arched proximodistally, and flexure is prominent near the base of the scapula. The suture between the scapula and coracoid is indistinct on all specimens. A very large acromion process is preserved on IGM 100/976 and IGM 100/986 (figs. 2, 4). The lateral surface of the acromion is transversely concave and the anterior surface is pitted for muscle insertion. In anterior view, the acromion is concave.

IGM 100/986 has a glenoid fossa with a



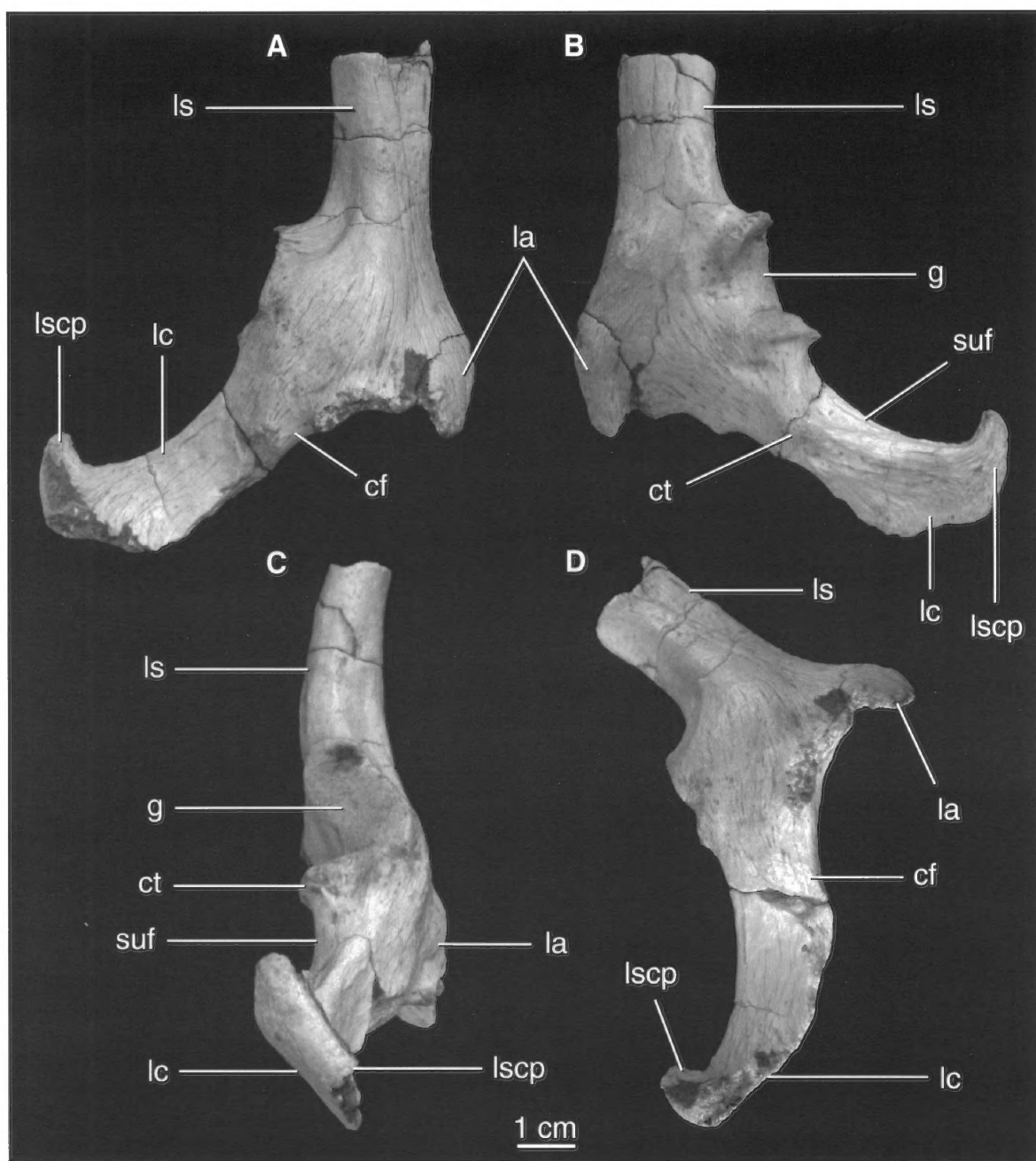


Fig. 4. Left scapulacoracoid of IGM 100/986. A, medial; B, lateral; C, posterior; D, anteromedial oblique views. Labels are spelled out in appendix 2.

laterally directed osseous floor, in contrast to the primitive theropod condition where the glenoid faces posteroventrally (fig. 4). The glenoid is defined dorsally and anteriorly by small ridges. Although damaged, the glenoids of IGM 100/976 and 100/982 also have laterally directed glenoid-humeral articulations.

The coracoids are large and quadrangular. Just ventral to the glenoid, the coracoid thickens and widens. The misnamed "biceps" tubercle (probably for insertion of the *M. coracobrachialis* [Makovicky and Sues, 1998], which is referred to here as the coracoid tubercle [sensu Osmólska et al., 1972]) lies on this thick area. The coracoid foramen

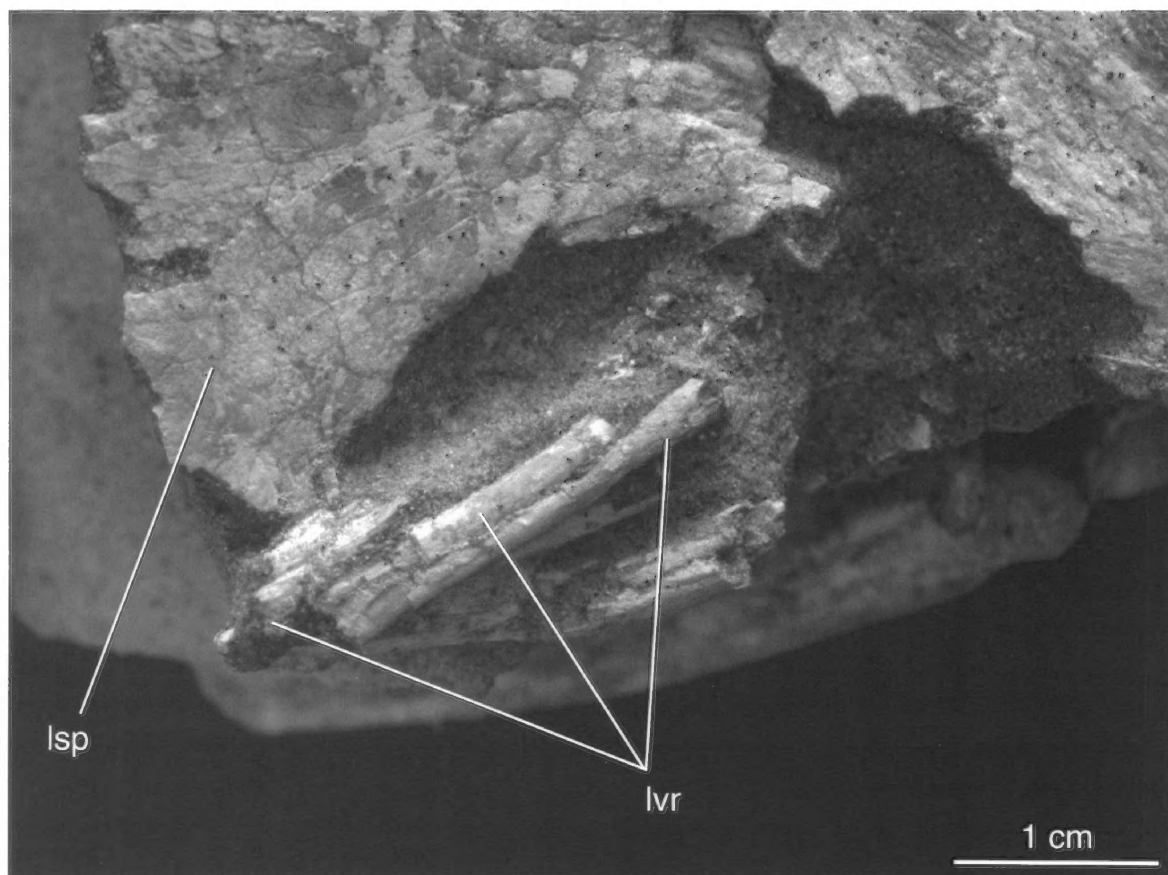


Fig. 5. Detail of three sternal ribs that articulated with the sternal plate in IGM 100/976. Right ventral view. Labels are spelled out in appendix 2.

lies dorsal and medial to the coracoid tubercle on IGM 100/976 and IGM 100/986. The posterolateral surface of the coracoid forms a broad, arched fossa (the subglenoid fossa); in other theropods, for which the coracoid is known (except for *Deinonychus antirrhopus* [Ostrom, 1974]), this surface is relatively thin. As seen in IGM 100/976, IGM 100/986, and IGM 100/982 the coracoid bends sharply at its ventral border, giving it an "L" shape in posterolateral view (figs. 2, 4, 7). This flexure allows the coracoid to articulate with the anterolateral margin of the sternal plates in a configuration reminiscent of that in *Archaeopteryx lithographica* (Tarsitano and Hecht, 1980: fig. 2; Wellnhofer, 1993: fig. 16).

The furcula of IGM 100/976 is a thin, boomerang-shaped bone (Norell et al., 1997). It consists of two lateral processes joined at the apex (fig. 3). The lateral rami are arched, giv-

ing each ramus a concave dorsal surface. The angle between the lateral rami is approximately  $107^\circ (\pm 3^\circ)$ . The bone is circular in cross section for most of the length of the ramus. However, the shafts flatten to a point that forms the articulating (epicleidial) surface (also seen on the left ramus of the fragmentary furcula in IGM 100/982 [fig. 7]) where the furcula presumably articulated with the acromion. Near the midline at the apex of the furcula, the bone also slightly flattens, assuming an oval cross section. At the apex, a small hypocleidium projects posteroventrally from the apex. The maximum length of this structure cannot be accurately determined because of incomplete preservation. There is no indication of a connection between the hypocleidium and the sternal plates, nor are any pneumatic foramina apparent.

In summary, the shoulder girdle of *Velo-*



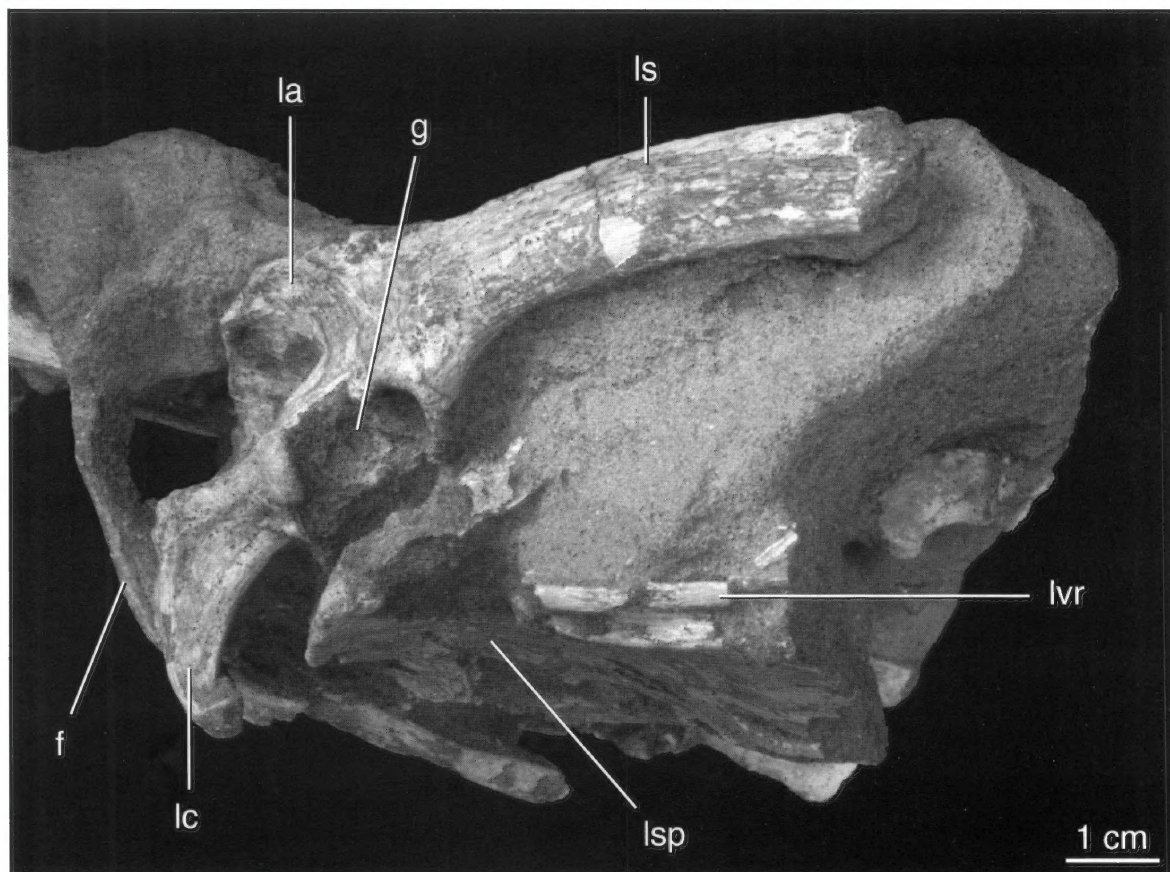


Fig. 6. Left lateral view of IGM 100/976. Labels are spelled out in appendix 2.

*ciraptor mongoliensis* is a unit of tightly articulated elements with a laterally projecting glenoid. The scapulocoracoids are bound to the anterior edge of the sternal plates and are bridged by the furcula. The L-shaped flexion of the coracoids determines the orientation of the scapular blade, which lies in a subhorizontal position high on the lateral side of the rib cage as seen in IGM 100/986 and IGM 100/982 (see below). This position is more horizontal and dorsal than that reported in other nonavian theropods (Makovicky and Currie, 1998), with the probable exception of *Unenlagia comahuensis* (Novas and Puerta, 1997; see below).

#### THE FORELIMB

Unfortunately, a complete, well-preserved humerus is not present in our collections. Both humeri are poorly preserved in IGM 100/982, and fragments are present in 100/986, 100/976, and 100/985. The proximal

head of the humerus is large and laterally inflected. It is delimited from the shaft of the humerus by a small groove (IGM 100/976) as in some other maniraptorans (Makovicky and Sues, 1998). The proximal end is concave anteriorly. The deltopectoral crest is expanded (IGM 100/982). A short groove is present on the humeral shaft, just distal to the deltopectoral crest on the posterolateral surface of the humerus (IGM 100/982, IGM 100/985) as in *Deinonychus antirrhopus* (AMNH 3015). This groove is confluent with a small rugose ridge distally (IGM 100/982, IGM 100/985). A small vascular foramen lies on the posterior surface just distal to the deltopectoral crest.

IGM 100/986 preserves the distal end of the left humerus although this element is in poor condition and slightly pathologic. It is similar to *Deinonychus antirrhopus* (see Ostrom, 1969a: figs 55, 56) in that the radial condyle is wider than the ulnar and concave anteriorly on the articular surfaces.



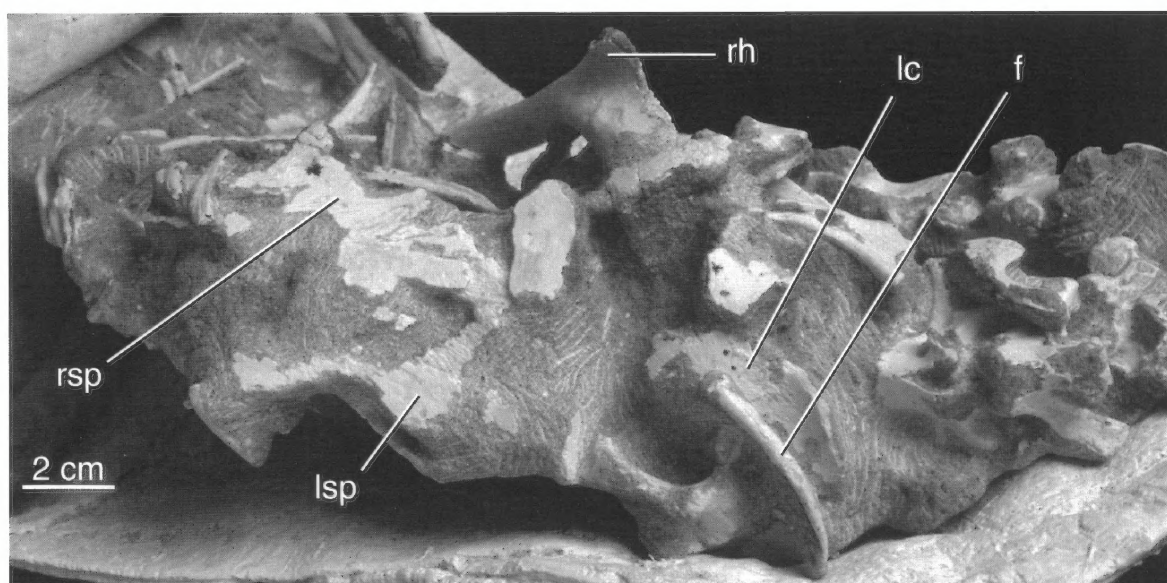


Fig. 7. Anterior thoracic region of IGM 100/982 in oblique right ventral view. Labels are spelled out in appendix 2.

Both ulnae are preserved on IGM 100/982, although all of the articular surfaces are damaged. All that can be determined from these elements is that the ulna is distinctly bowed, as is typical of maniraptorans (Gauthier, 1986), and is more massive than the radius. The proximal ends of both ulnae are preserved on IGM 100/986. The ends are subtriangular in proximal view. A large, thin olecranon process forms a longitudinal keel along the proximoventral margin of the preserved section of the ulna. The lateral surface and ventral edge of the olecranon process are pitted and rugose and suggest insertion for the triceps tendon. The left, better preserved element shows that the dorsal surface of the olecranon fossa is actually formed by two cotyles; the lateral one is slightly convex, forming a small bump, whereas the medial one is a small concave depression. On the dorsal surface of the ulna just anterior and between the two cotyles lies a small longitudinal tubercle, which suggests an insertion point for a tendon of an antebrachial muscle.

The proximal end of the radius is preserved in IGM 100/986, although it is heavily eroded. Complete radii lacking articular surfaces are preserved in IGM 100/982. These lack much in the way of morphology

except that the shafts are lateromedially flattened distally as in *Deinonychus antirrhopus*.

A fully articulated right manus is preserved on IGM 100/982 (fig. 8), and manual elements are associated with other specimens (IGM 100/986 and 100/985) (table 1). A penultimate phalanx and ungual of digit III was found with the type of *Velociraptor mongoliensis* (AMNH 6515) (fig. 9). The manus shows the typical theropod phalangeal formula. Digit II is the longest, and digit I is shorter than digit III. Metacarpal I is short and robust. It is dorsoventrally flattened and twisted. Metacarpal II is the longest of the three metacarpals, and is slightly concave ventrally. The distal articulation of metacarpal II is ginglymoid (as are the distal articular surfaces of all the metacarpals); the medial condyle is larger, forming an elevated bump on the dorsal surface of the element.

Metacarpal III is slender, and its proximal end is displaced ventrally relative to metacarpals I and II. Phalanx I-1 is the most robust and curves laterally along its median axis. There are no extensor pits distally. The ungual of digit 1 is the largest of the three unguals. It bears a prominent flexor tubercle, and is narrow mediolaterally. The groove for the keratinous claw on the medial surface is

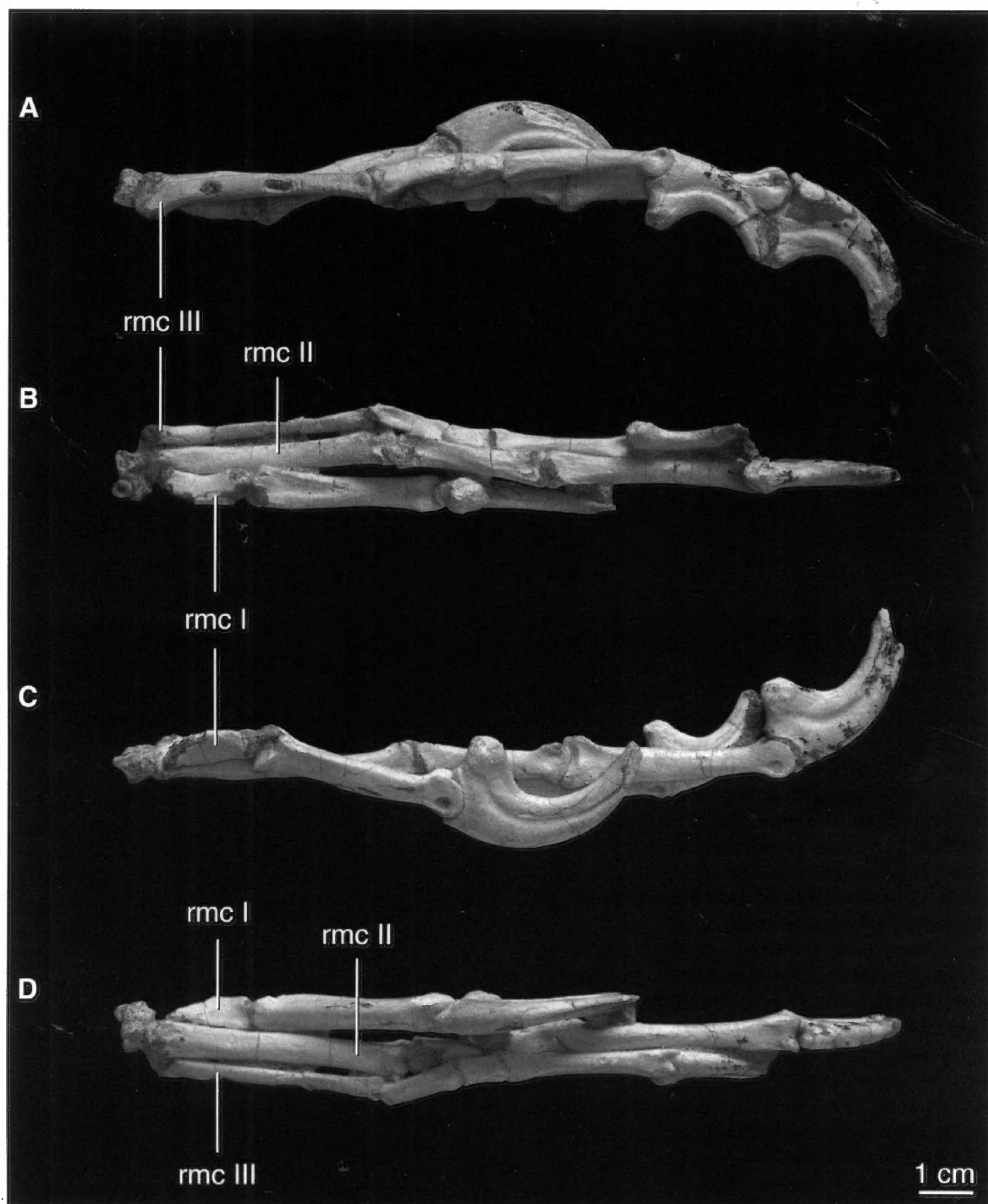


Fig. 8. Right manus of IGM 100/982. A, lateral; B, ventral; C, medial; D, dorsal views. Labels are spelled out in appendix 2.



dorsal to the corresponding groove on the lateral surface. Phalanx II-1 is difficult to observe on IGM 100/982; however, it is well preserved in IGM 100/986. It is robust and nearly symmetrical. The proximal articular surface is ridged to allow for a ginglymoid articulation. The distal articulation is also ginglymoid but the lateral condyle is slightly larger than the medial; on the lateral and medial surfaces, the collateral ligament pits are shallow. A small foramen lies on the ventromedial surface of the shaft. The ventral surface is slightly concave proximally in lateral view.

Phalanx II-2 is also well preserved on IGM 100/986. It is laterally compressed proximally, and bears a ridge on the dorsal surface of the element, just distal to the proximal articulation. The proximal articular surface is asymmetrical, the medial surface being smaller than the lateral. There is a shallow extensor pit just posterior to the distal articulation on the dorsal surface of the element. The collateral ligament pits are deep and situated dorsally on the lateral face of the distal articulation. The ungual phalanx is similar to that of digit I except being slightly smaller.

Phalanx III-1 is short, but not as short as III-2. It is angular in cross section, with the ventral surface concave. The phalanx also has a ventrally concave surface anteroposteriorly. The proximal articulation is asymmetric so that the lateral surface is larger than the medial one; the lateral surface is more extensive distally. The distal articulation is ginglymoid and slightly asymmetric. This asymmetry of the articular surfaces in digit III may account for the pronounced medial pronation of this digit as preserved in many maniraptoran specimens (Wagner and Gauthier, 1999). The dorsal surface of the bone has a poorly developed longitudinal ridge.

Phalanx III-2 of IGM 100/986 is the shortest phalanx of the hand. It has a highly asymmetrical proximal articulation. The distal articulation is not well preserved on any of the available specimens. Phalanx III-3 of IGM 100/986 is elongate, relatively straight, and symmetric along its median longitudinal axis with a longitudinal ridge on the ventral surface of the shaft. The proximal condyle is ginglymoid and asymmetrical as in III-1 and



Fig. 9. Ungual and penultimate phalanx of digit III of *Velociraptor mongoliensis* (AMNH 6515).

III-2. This asymmetry extends to the lateral surface of the phalanx where a small bump is present adjacent to the proximal end. The ungual is the smallest of the three manual unguals and shaped like the other two. Among all specimens of *Velociraptor mongoliensis* examined here, moderate variation occurs in the morphology of the flexor tubercles of the manual unguals.

#### THE HIND LIMB

The femur and tibia of IGM 100/986 are well preserved (figs. 10–12) with little post-mortem distortion beyond cracking (table 2). The femur is distinctly anteriorly bowed as in avialans (e.g., *Shuvuuia deserti*, *Mononykus olecranus*, *Archaeopteryx lithographica*, *Patagopteryx deferrariisi*, and others). The proximal end of the femur includes the femoral head, which is subspherical and perforated by a small pit. Posteriorly the head is bordered by a deep groove. Ventrally and anteriorly the femoral neck is short. Dorsally

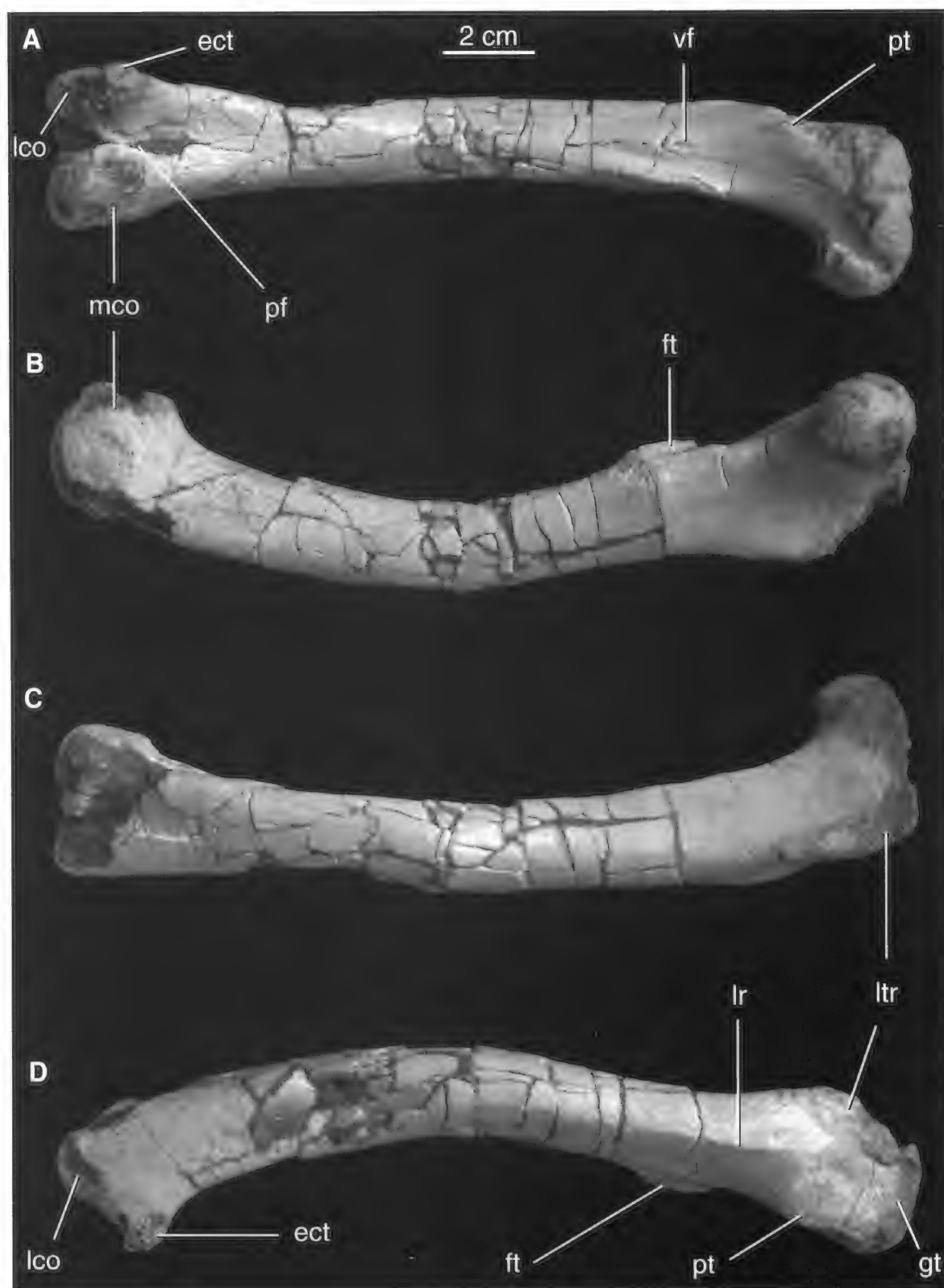


Fig. 10. Left femur of IGM 100/986. A, posterior; B, medial; C, anterior; D, lateral views. Labels are spelled out in appendix 2.



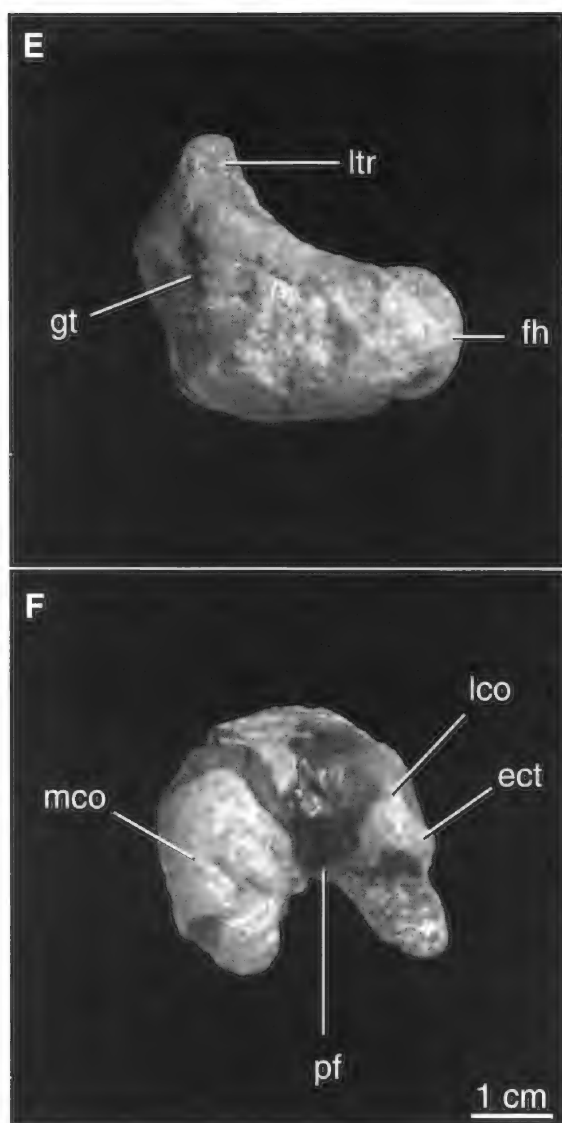


Fig. 10. *continued*. Left femur of IGM 100/986. E, proximal; F, distal views. Labels are spelled out in appendix 2.

the femoral head is confluent with the greater trochanter. Although not fully preserved, the greater and lesser trochanters appear to be appressed but separated by a small groove as in *Deinonychus antirrhopus* (Ostrom, 1976a) and *Archaeopteryx lithographica* (Ostrom, 1976b; see fig. 17 in Norell and Makovicky [1997]). This groove, which is parallel to the long axis of the bone and adjacent to the edge of the lesser trochanter, extends approximately 1.5 cm down the lateral surface of the femoral shaft.

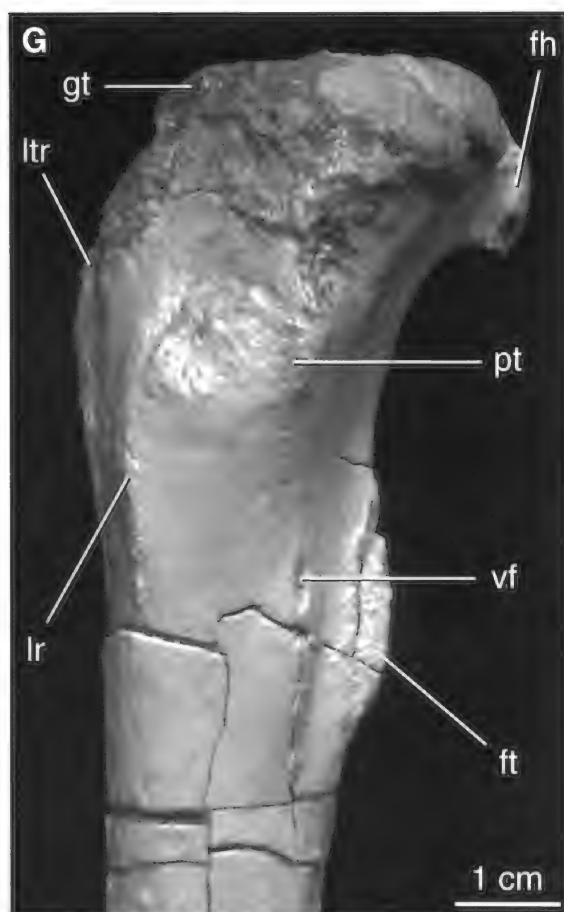


Fig. 10. *continued*. G, Left femur of IGM 100/986 in posterolateral oblique view of proximal end showing the presence of a large fourth trochanter (ft). Labels are spelled out in appendix 2.

A distinct posterior trochanter is present on the lateral surface as a small ridge forming the angle between the lateral and posterior surfaces of the femur. Proximally, on the lateral surface of the femur lies a large rugose bump (the lateral ridge) bounded dorsally by a shallow depression. Ventrally the lateral ridge grades into a well-defined ridge that is confluent with the intermuscular line running along the long axis of the femur to the lateral condyle. Unusually for dromaeosaurids (Ostrom, 1990), a well-developed fourth trochanter is present as a large crest on the posteromedial angle of the femur. A distinct fourth trochanter is also present in an identical position in IGM 100/982. A large vascular foramen is present on the posterior

TABLE 1  
Measurements of the Hand in *Velociraptor mongoliensis* (in millimeters)

	IGM 100/982, right	IGM 100/986, left	AMNH 6515, right		IGM 100/982, right	IGM 100/986, left	AMNH 6515, right
METACARPALS				PHALANGES			
Metacarpal I				II3			
Length	19.2 <sup>a</sup>			Length along outer curve		48.8	45.0
Distal transverse width	7.3 <sup>a</sup>	10.5		Proximal height	19.1	20.0	17.1
Proximal transverse width		11.3		Height of facet	9.0	10.9	1.2
Metacarpal II				Proximal transverse width	5.3	8.0	3.3
Length	50.8			Width at flexor tubercle	5.1	6.7	5.0
Distal transverse width	7.0			III1			
Proximal transverse width	8.7			Length	17.6	19.0	
Metacarpal III				Distal transverse width	4.6	5.2	
Length	45			Proximal transverse width	4.5	5.6	
Distal transverse width	5.0			Proximal height	7.0	7.9	
Proximal transverse width	4.6 <sup>a</sup>			III2			
PHALANGES				Length	10.1	11.1	
I1				Distal transverse width	5.0		
Length	39.9 <sup>a</sup>	47.1		Proximal transverse width	4.8	6.0	
Distal transverse width	7.9	8.0		Proximal height	7.0	8.0	
Proximal transverse width	8.8	7.9		III3			
Proximal height	9.3	11.6		Length	32.2	33.2	
I2				Distal transverse width	5.1	6.0	
Length along outer curve	39.9 <sup>a</sup>			Proximal transverse width	6.1		
Proximal height	18.9			Proximal height	7.0	8.2	
Height of facet	10.0			III4			
Proximal transverse width	7.8			Length along outer curve	32.0		
Width at flexor tubercle	7.8	8.3		Proximal height	16.7	17.1	
II1				Height of facet	8.0	8.4	
Length	31.3	33.2		Proximal transverse width	4.5	6.0	
Distal transverse width	6.8	8.0		Width at flexor tubercle	5.6	5.3	
Proximal transverse width	8.0	8.0					
Proximal height		11.4					
II2							
Length	45.8						
Distal transverse width	7.0						
Proximal transverse width	7.2						
Proximal height	11.0						

<sup>a</sup> Estimated values.

face of the femur, level with the fourth trochanter as in many other theropods (Perle et al., 1994; Madsen, 1976).

The distal end of the femur is composed of two large condyles separated posteriorly by a deep popliteal fossa that is not closed distally by medial and lateral expansions of the distal condyles. The buttresses to the condyles are not extensive proximally on the

posterior shaft of the femur. The lateral condyle is slightly larger than the medial one. The ectocondylar tuber of the lateral condyle is deflected laterally.

The tibial shaft is straight and round in cross section for most of its length, becoming oval to subtriangular distally. The proximal end is expanded and bears a well-developed single cnemial crest (IGM 100/986) (fig. 11).



TABLE 2  
Measurements of Hindlimb in  
*Velociraptor mongoliensis* (in millimeters)

	IGM 100/985		IGM 100/986	
	right		right	left
Femur				
Length				238
Distal transverse width			34.3	33.7
Distal length			33.9	33.3
Proximal transverse width				36.5
Proximal anteroposterior length				34.2 <sup>a</sup>
Least diameter of shaft				16.7 <sup>a</sup>
Tibiotarsus				
Length				255
Greatest distal transverse width	29.4		38.7	38.1
Greatest distal depth			21.3 <sup>a</sup>	22.4
Greatest proximal transverse width			47.0	47.8 <sup>a</sup>
Greatest proximal depth			25.5	27.3
Least diameter of shaft				16.3 <sup>a</sup>
Ascending process of astragalus length			51.4 <sup>a</sup>	
Fibula				
Width at narrowest point	2.7 <sup>a</sup>			2.6
Proximal length			28.6	
Width at narrowest point on proximal end			7.7	

<sup>a</sup> Estimated values.

This crest is unusual in that it bears a large rugose boss, which is oriented laterally and separated from the anterior edge by a shallow sulcus. This contrasts with the primitive theropod condition where the anterior edge of the cnemial crest is hooked laterally and lacks a rugose boss. The cnemial crest extension onto the tibial shaft is limited. Posteriorly, the triangular proximal articular surface of the tibia is expanded to overhang the tibial shaft. Small, but well-developed, lateral and medial condyles separated by a shallow groove correspond to the articular surfaces of the femur. The lateral condyle of the femur articulates between the lateral condyle and the fibular head. The proximal articular surface extends onto the lateral face of the tibia, where it meets the fibula. The fibular crest is short (less than 20% of tibial length) and placed proximally. The tibiotarsus is longer than the femur (table 2). Additional aspects of the dromaeosaurid tibia were discussed in

Norell and Makovicky, 1997 (see also Ostrom, 1976b, 1990).

The tibia flares widely distally. The astragalus forms most of the distal articulating surface of the tibiotarsus, although it only wraps onto the posterior face of the tibia to a very minor degree. The astragalus bears a well-developed ascending process that is taller laterally than medially on the anterior surface of the tibia. Laterally, the ascending process buttresses the distal part of the fibula (fig. 12), a condition that is also apparent in both IGM 100/985 and IGM 100/986. The ascending process is separated from the body of the astragalus by a deep groove. The articular surface of the astragalus is composed of a large medial condyle separated by a shallow cleft, but confluent with a small lateral condyle. Part of this lateral condyle is undoubtedly formed by the calcaneum, which is fused to the astragalus. A faint depression (especially in IGM 100/986) that may be a remnant of the boundary between these individual bones is present. Complete fusion of these elements is seen in all specimens of *Velociraptor mongoliensis* where these structures are preserved, except for the left side of IGM 100/982 where fusion may not be complete. Nevertheless, fusion between these elements is far more complete than the unfused condition reported for *Deinonychus antirrhopus* (Ostrom, 1969a, b). On the lateral surface of the tibiotarsus, a small triangular pocket is formed by the calcaneum, tibial shaft, and ascending process of the astragalus. Apparently it received the distal end of the fibula. However, in neither of the well-preserved tibiotarsi, which preserve the distal end of the fibula (IGM 100/985 and IGM 100/986), does this element reach this supposed articulation point.

The proximal end of the fibula is crescentic with the medial face concave (fig. 13). A deep fibular fossa, as in ornithomimids (Serenó et al., 1996) is absent. Posteriorly a small ridge descends from the proximal articular surface bounding a small depression medially. The iliofibularis tubercle forms a small expanded area on the proximolateral surface. The fibula rapidly attenuates to a delicate rod below the proximal end. The shaft of the fibula appears solid where its cross section is



Fig. 11. Left tibiotarsus of IGM 100/986. A, anterior; B, lateral; C, posterior; D, medial views. Labels are spelled out in appendix 2.



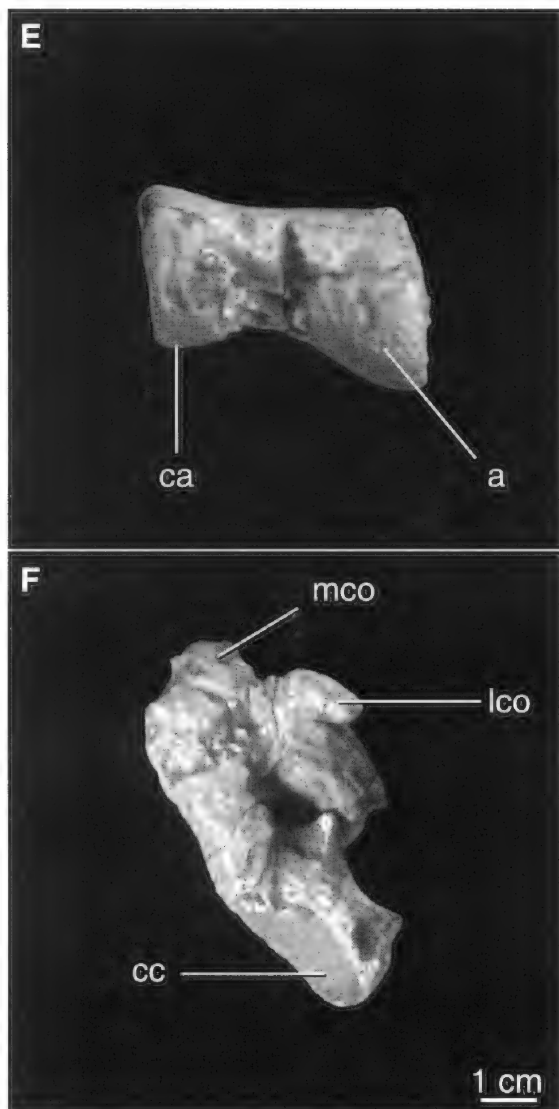


Fig. 11. *continued.* Left tibiotarsus of IGM 100/986. **E**, distal articular surface; **F**, proximal articular surface. Labels are spelled out in appendix 2.

revealed by breakage in IGM 100/985 and IGM 100/986.

Major discussions of the pes in dromaeosaurids can be found in Ostrom (1969a) and Norell and Makovicky (1997). The well-preserved feet of IGM 100/986, however, allow us to make a few further points (table 3). The fusion between the distal tarsal and the metatarsals (mentioned in Norell and Makovicky, 1997) is shown in figures 14 and 15. The preserved proximal end of the right foot clearly shows that the two distal tarsals are

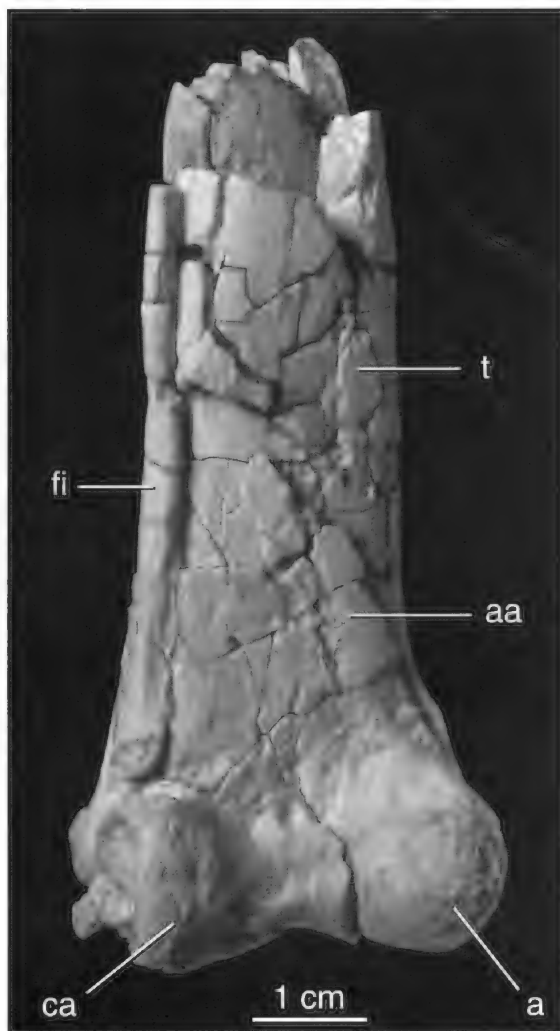


Fig. 12. Right distal tibiotarsus of IGM 100/986 showing buttressing of distal fibula by lateral margin of ascending process of astragalus. Labels are spelled out in appendix 2.

completely fused to each other and incompletely fused to corresponding metatarsals III and IV. Fusion is most apparent between the lateral distal tarsal (see Norell and Makovicky, 1997) and the lateroproximal surface of metatarsal IV. There the distal tarsal overhangs the margin of mt IV and buttresses the proximal end of metatarsal V. Anteriorly, the distal tarsal fails to reach the anterior margin of the proximal surface of metatarsal IV. Medially, the medial distal tarsal can best be viewed on the left foot of IGM 100/986 where it fails to reach the anterior edge of the proximal surface of metatarsal III. Pos-



Fig. 13. Left proximal fibula of IGM 100/986. A, lateral; B, medial views.

teriorly, it is strongly fused to metatarsal III and overhangs its posterior edge. A small flange of the medial distal tarsal overhangs the proximal surface of metatarsal II posteriorly.

The left foot of IGM 100/986 (fig. 16) and both feet of IGM 100/982 corroborate our previous finding that pedal digit I is not reversed, but lies laterally and high on the metatarsus as in other nonavian theropods (Norell and Makovicky, 1997).

#### PELVIC GIRDLE

Although a detailed description of the pelvis was published by Norell and Makovicky (1997), the well-preserved specimen of a larger individual, IGM 100/986 provides additional new information (table 4). As in IGM 100/985 (Norell and Makovicky, 1997), the ilia are low in lateral view (fig. 17). The iliac surface dorsal to the acetabulum is laterally concave. The dorsal border of the ilia displays the same sinuous outline present in IGM 100/985. The antiliac shelf that forms the cuppedicus fossa typical of tetanuran ilia is reduced, evident only as lateral flexion of the ventral border of the ilium that wraps

onto the pubic peduncle (fig. 18). The pelvis of IGM 100/982 is identical to the two specimens described earlier for these characteristics. A poorly defined vertical crest above the acetabulum that divides the anterior and posterior muscle fossae on the lateral surface of the pelvis is present on IGM 100/982 but is absent on other specimens.

In IGM 100/986, the sacrum is formed of six co-ossified vertebrae (fig. 17). In IGM 100/985, the sacrum consists of five sacra, but the first caudal is in close proximity with the iliac blades, suggesting that this vertebra may be incorporated into the sacrum later in ontogeny. This is confirmed by our observations in IGM 100/986, a larger specimen, where the first caudal was fused to the fifth sacral through the centrum and distal transverse processes. The neural spines of the first five sacra co-ossify to form a continuous lamina. The neural spine of the posterior sacral appears not to participate in this structure. A pneumatic foramen is only present on the centrum of the second sacral of IGM 100/986.

The pubes are nearly identical to those of IGM 100/985. They are long and fused dis-

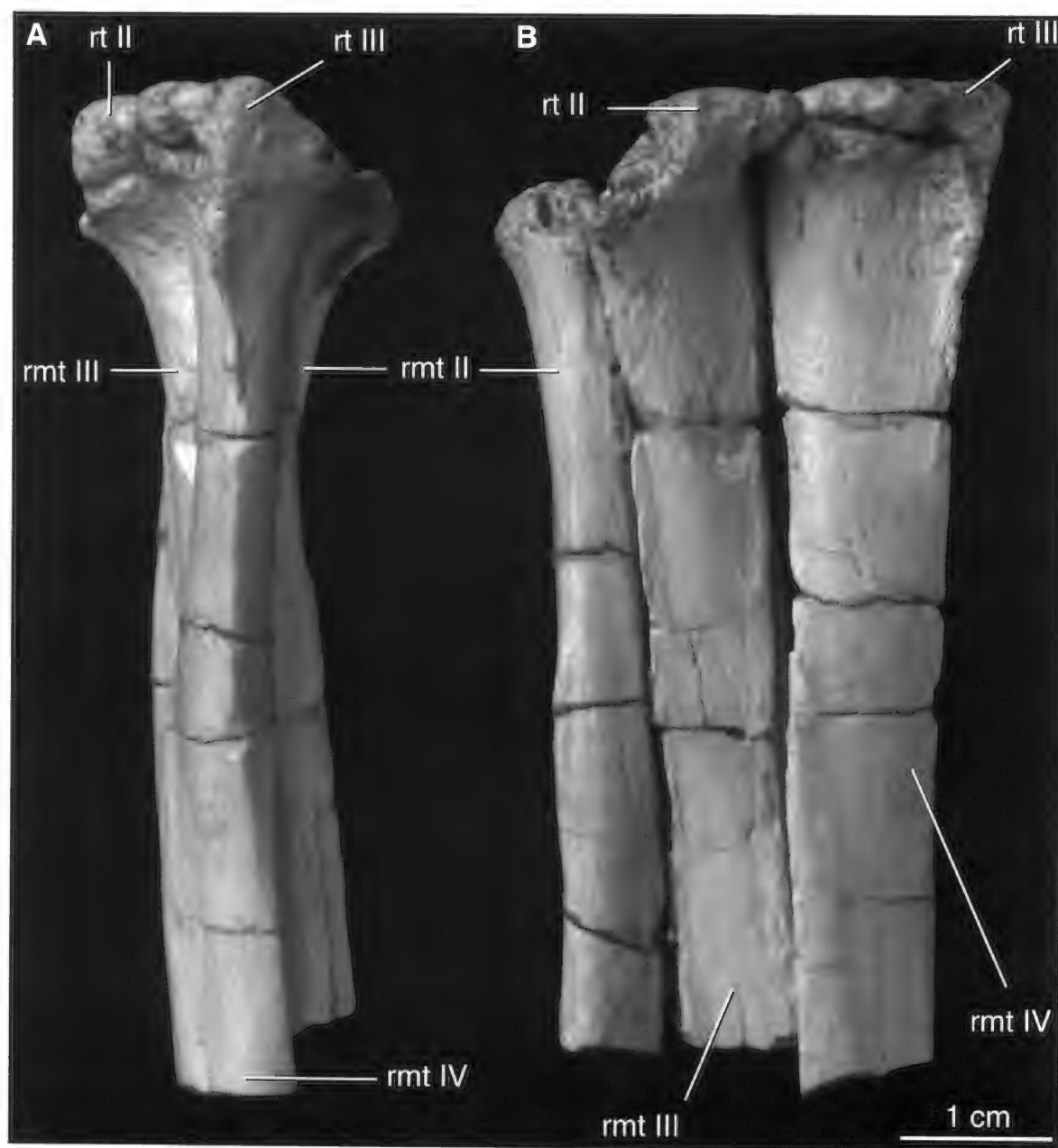


Fig. 14. Right metatarsals and distal tarsals of IGM 100/986. A, lateral; B, posterior views showing extensive degree of fusion between distal tarsals and metatarsals.

tally. Notably, although somewhat flattened, the pelvis is demonstrably opisthopubic. Despite the distortion present in IGM 100/986, reconstruction of the acetabulum as a circular opening requires a posterior direction for both the pubis and the ischium—extending well behind a perpendicular plane drawn

from the horizontal sacral axis at its posterior end.

Distal expansion of the pubis forms a pubic boot with a small anterior component. Lateral to the pubic apron, just proximal to the pubic boot, well-defined ridges lie at the posterolateral edge of the pubes. The pres-



TABLE 3  
Measurements of Foot in *Velociraptor mongoliensis* (in millimeters)

	IGM 100/982		IGM 100/985		IGM 100/986		AMNH 6518
	right	left	right	left	right	left	right
DISTAL TARSALS							
Lateral tarsal							
Length (proximodistal)					4.8		4.7 <sup>a</sup>
Transverse width					17.9 <sup>a</sup>		
Anteroposterior width					13.6		
Medial tarsal							
Length (proximodistal)				4.2			4.1
Anteroposterior width						14.9	
METATARSALS							
Metatarsal I							
Length	22.5		22.0	21.4		27.9	
Distal transverse width		7.2		5.8		6.8	
Distal depth		7.4	6.7	6.6		7.6	
Metatarsal II							
Length		73.7	71 <sup>a</sup>	71.2		84.8	
Distal transverse width	9.4	9.2		8.9	11.3	12.2	
Distal depth		9.9		10.6	12.0	14.3	
Proximal transverse width					12.4	14.1	
Proximal depth					17.4	19.2	
Metatarsal III							
Length			85.6 <sup>a,b</sup>	86.2		99.1	
Distal transverse width		12.8		12.8	15.1	14.2	
Distal depth				14.9	16.2	16.8	
Proximal transverse width				11.9 <sup>a</sup>	13.4	14.2	
Proximal depth					21.8	22.0	
Metatarsal IV							
Length		83.4	79.0	78.2		91.6	
Distal transverse width				11.1	17.3	13.4	
Distal depth				12.3	16.6	16.9	
Proximal transverse width					18	19.8	
Proximal depth					15.4	15.8	
Metatarsal V							
Diameter				2.9 <sup>c</sup>		3.6 <sup>a</sup>	4.1
Length		>29.8		>31.7 <sup>b</sup>			40.1
PHALANGES							
I1							
Length	19.8	19.3		16.9 <sup>b</sup>			16.2
Distal transverse width	4.9			4.9			4.8
Proximal transverse width	7.2			6.3			
Proximal height				6.1			
Distal height	5.3	6.0		5.8			6.9
I2							
Proximal transverse width				3.6			4.6
Proximal height		10.0	8.4	8.5			13.0
Facet height		8.4	7.0	7.1			8.9

TABLE 3  
*Continued*

	IGM 100/982		IGM 100/985		IGM 100/986		AMNH 6518
	right	left	right	left	right	left	right
PHALANGES ( <i>continued</i> )							
II1							
Length		23.9		23.6 <sup>b</sup>		26.6	
Distal transverse width		10.8		10.2			
Proximal transverse width				11.2	12.1	12.6 <sup>d</sup>	
Proximal height		10.1 <sup>a</sup>		9.6	13.0	13.2	
Distal height		9.8		8.9		10.1	
II2							
Length		26.1	24.2	24.0		28.0	
Distal transverse width			7.0	6			
Proximal transverse width		9.3		8.11			
Proximal height		12.4		12.1		14.8	
Distal height			11.1	11.0		13.6	
II3							
Length along outer curvature		66.3 <sup>a</sup>	64.8				
Proximal transverse width	7.2	7.1 <sup>a</sup>	7.1	6.1		9.9	
Proximal height	22.3 <sup>a</sup>	22	18.7	18.3		23.4	23.1
Facet height	15.8 <sup>a</sup>	15.1	13.0	12.9		15.5	16.8 <sup>a</sup>
III1							
Length		39.6		37.6		44.0	
Distal transverse width		12.3	13.8 <sup>a</sup>	11.2		13.6	
Proximal transverse width				13.3			
Proximal height				12.4	16.1	15.5	
Distal height		9.9	9.5 <sup>a</sup>	10.8		11.5	
III2							
Length			24.7	24.9 <sup>b</sup>		27.4	
Distal transverse width				9.4		12.8	
Proximal transverse width		11.1		11.4		13.6	
Proximal height		10.7	10.0	10.1		13.4	
Distal height			8.9	8.6		10.0	
III3							
Proximal height						12.2	
III4							
Length along outer curvature				32.3			
Proximal transverse width				7.0			
Proximal height				12.3			
IV1							
Length		27.1 <sup>a</sup>		26.8		30.1	
Distal transverse width		11.1		9.4	12.1	11.8	
Proximal transverse width				12.3		11.9 <sup>a</sup>	
Proximal height				11.5		14.0	
Distal height				9.1	10.5	11.0	
IV2							
Length			21.0	21.3		23.0	
Distal transverse width				8.6		10.5	
Proximal transverse width				9.5		11.1	
Proximal height				9.6		14.2	
Distal height			8.2	8.3		8.6	

TABLE 3  
*Continued*

	IGM 100/982		IGM 100/985		IGM 100/986		AMNH 6518
	right	left	right	left	right	left	right
PHALANGES ( <i>continued</i> )							
IV3							
Length			17	16.8		18.6	
Distal transverse width			8.4	8.0	1.4	9.4	
Proximal transverse width				8.9		9.9	
Proximal height				8.9		12.7	
Distal height			7.2	7.0	8.6	8.4	
IV4							
Length			16	16.1 <sup>b</sup>	19.6	18.6	
Distal transverse width			6.2	6.8	9.8	9.1 <sup>d</sup>	
Proximal transverse width			7.3 <sup>a</sup>	7.8	10.1	8.2 <sup>d</sup>	
Proximal height				8.4	10.3	11.0	
Distal height			7.2 <sup>a</sup>		8.1	8.0	
IV5							
Length along outer curvature			32.3	31 <sup>a</sup>			
Proximal transverse width			6.9	7.1		7.4 <sup>a</sup>	
Proximal height				12.3		13.8	
Facet height			9.2	8.9		11.5	

<sup>a</sup> Estimated values.  
<sup>b</sup> Modification from Norell and Makovicky.  
<sup>c</sup> Widest dimension.  
<sup>d</sup> Slight pathology.

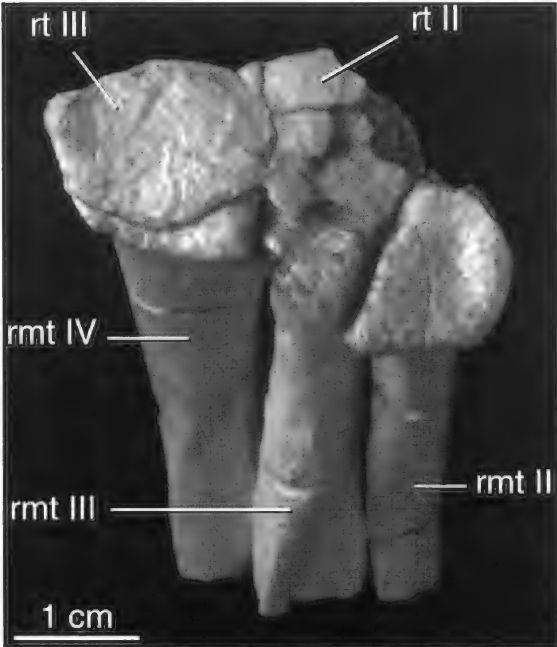


Fig. 15. Distal right ankle of IGM 100/986 showing position of tarsals relative to corresponding metatarsal elements.

ence of a hypopubic cup (Tarsitano and Hecht, 1980) cannot be demonstrated with certainty in these specimens (see discussion below). However, both IGM 100/985 (fig. 19) and IGM 100/986 appear to possess such a concave structure on the posterior surface of the distal expansion of the pubic symphysis. Nevertheless, this apparent morphology may be influenced by postmortem effects (i.e., arthropod damage).

Like IGM 100/985, the ischia of 100/986 are not fused distally and they twist ventrally so that their distal extremities lie in a horizontal plane.

DORSAL VERTEBRAE

Six posterior dorsal vertebrae are present in articulation with the sacrum on IGM 100/986 (fig. 20). Three additional vertebrae (anterior dorsals) were found articulated to one another as float near the specimen (table 5).

The three isolated vertebrae have pneu-



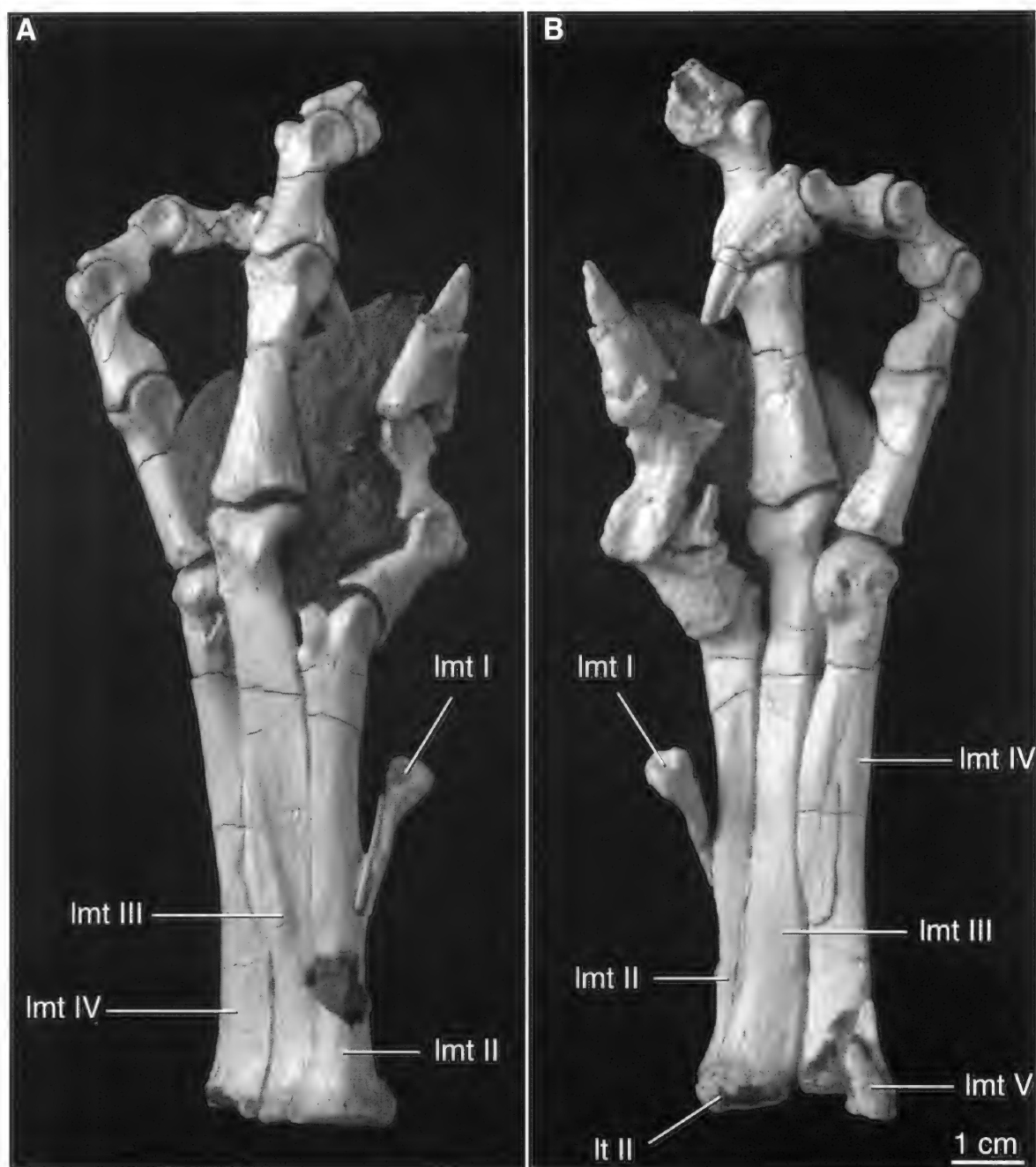


Fig. 16. Left pes of IGM 100/986. A, anterolateral oblique; B, ventromedial oblique views.

matic centra with a honeycombed internal structure. The neural canal is very wide in comparison to other nonavian theropods. The most anterior of these vertebrae lacks most of the neural arch. The second of the series bears a prominent, moundlike hypapophysis and has parapophyses high on the centrum, suggesting that it represents the first

dorsal vertebra. The centrum is short, and without angles (i.e., the lateral and ventral surfaces are confluent), displaying a central surface like those of the cervical vertebrae. The last element of the series has a large rugose lip ventral to the anterior face of the centrum in place of a hypapophysis. A large pneumatic foramen (infrapostzygapophyseal

TABLE 4  
Measurements of Pelvic Girdle in *Velociraptor mongoliensis* (in millimeters)

	IGM 100/982		IGM 100/985		IGM 100/986	
	right	left	right	left	right	left
Ilium						
Length	131.7	124.6	126.8	132.8		145.8 <sup>a</sup>
Length anterior to acetabulum				64.9		59.7 <sup>a</sup>
Length posterior to acetabulum				57.9		68.2 <sup>a</sup>
Height above acetabulum		28.0		26.8		
Pubis						
Length (proximodistal)	132 <sup>a</sup>		167		213	208 <sup>a</sup>
Length (anteroposterior)	26 <sup>a</sup>	25.5	29.9		28.5	27.5 <sup>a</sup>
Length of pubic boot						34.6
Ischium						
Length (proximodistal)			97.7		115.1	118.8 <sup>a</sup>
Width across peduncles				28.3	35	35.9 <sup>a</sup>
Width across obturator process			39	37.0 <sup>a</sup>		
Obturator process apex to iliac peduncle				70 <sup>a</sup>		

<sup>a</sup> Estimated values.

foramen) invades the centrum below the base of the transverse process.

The centra of the posterior dorsals are short, platycoelous, and subcircular in cross section. Unlike those in *Deinonychus antirrhopus* (Ostrom, 1969a), they lack large pneumatic foramina. The intercentral faces are flared transversally. All of the dorsals have completely fused neurocentral sutures. Each vertebra bears a moderately tall neural spine, which is transversely expanded at the distal end. Unlike in ornithomimids and tyrannosaurids, the rugose ligament scars for the intraspinous ligaments fail to reach the tips of the neural spines. On the anteriormost vertebra of the posterior dorsal series, the transverse processes are elongated and incline slightly dorsoposteriorly. The transverse processes become shorter and less inclined as they approach the sacrum. The parapophyses of the dorsals are raised on a short stalk and are almost at an elevation level with the diapophyses. The postzygapophyses bear well-developed hyposphenes. The neural arches are pneumatic and bear pneumatic fossae.

Associated with the posterior dorsals are a few ribs. The terminal posterior dorsal rib merits comment in that it is single-headed and small. The remaining ribs are unremarkable in that they are double-headed and flat,

with tubercula and capitula lying at almost the same level when articulated, approaching the condition seen in avialans.

CAUDAL VERTEBRAE

The tail of IGM 100/986 is preserved in articulation following an S-shaped curve (fig. 21, 22). Surprisingly, this conformation of the tail seems not to disturb the arrangement of the elongate prezygapophyses, suggesting that there may have been substantial lateral mobility of the tail in life. The first 26 caudal vertebrae are preserved in articulation (table 5). It is difficult to determine how many additional vertebral elements were present (compared with an estimated 36 to 40 for *Deinonychus antirrhopus* [Ostrom, 1969a]). The first chevron of IGM 100/986 is situated between the last sacral and the first caudal. The anterior caudals were described by Norell and Makovicky (1997). If differences in the number of vertebrae incorporated into the sacrum are taken into account, this is the same as reported for IGM 100/985.

One of the remarkable features of the velociraptorine tail is the development of long, bifurcating prezygapophyses (fig. 22). In the tail, strong elongation of the prezygapophyses begins at vertebrae 10, and caudal 11 is

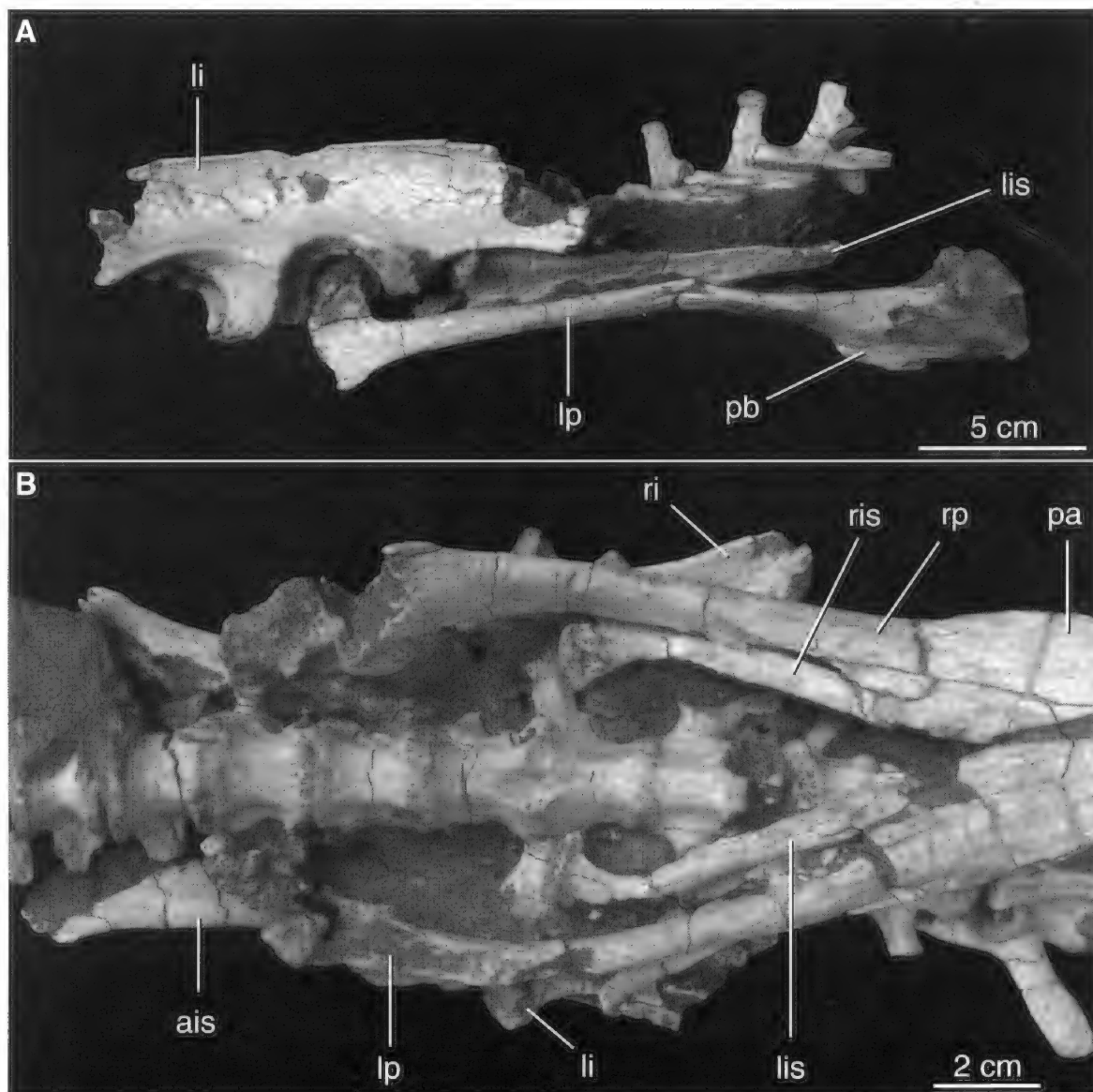


Fig. 17. Pelvic region of IGM 100/986. A, left lateral; B, ventral views. Labels are spelled out in appendix 2.

the last to bear transverse processes. The elongate prezygapophyses extend anteriorly to at least the level of the sixth caudal vertebra. Distal caudal vertebrae have elongate centra that are subcircular to square in cross section. Distal to caudal 14, the neural spine is only represented by a low, rounded ridge. The postzygapophyses of the distal caudals are small, closely spaced, and face ventrolaterally. A number of caudals display strong pathologic growths.

The caudal chevrons of the anterior caudal vertebrae are very broad. From the fifth chevron on, they become flared distally. Bifurcated, elongate chevrons extend anteriorly to at least the level of the eighth vertebra. Chevron 11 forms a horizontal triangular plate and is the first element to show elongate anterior processes. Chevrons 12, 13, and 14 have a ventral depression. Posteriorly the chevrons become flat, anteroposteriorly more elongate, and transversely narrow.



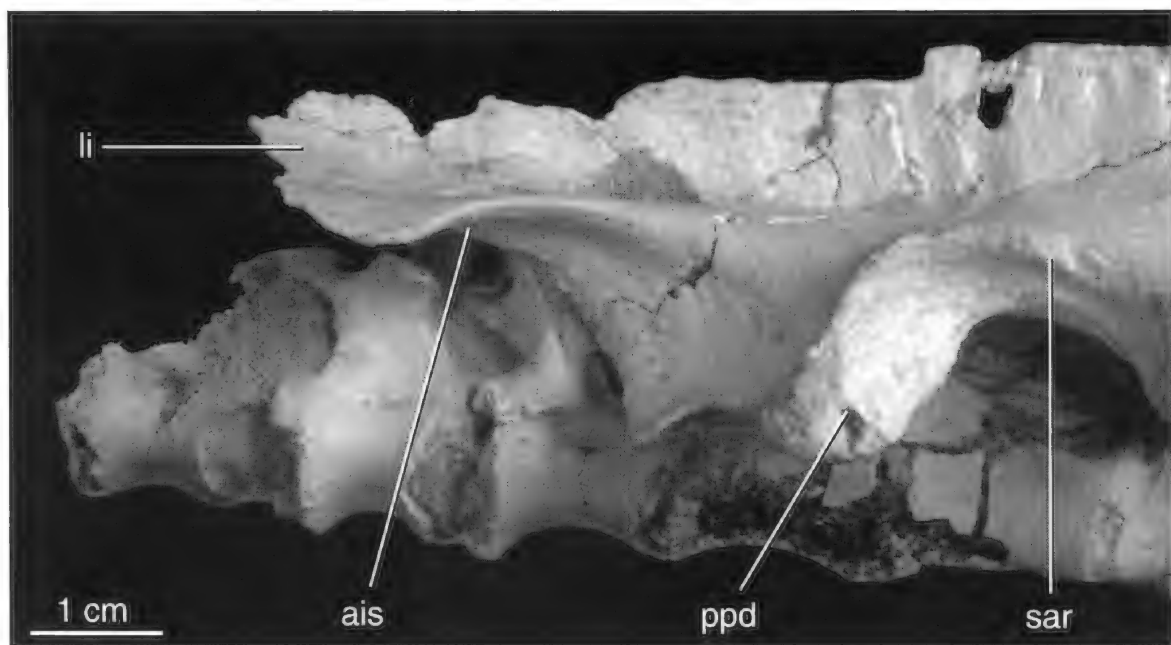


Fig. 18. Anterior left ilium of IGM 100/985 showing reduced antiliac shelf. Labels are spelled out in appendix 2.

## DISCUSSION

The paucity of described postcranial material for most other maniraptoran taxa precludes detailed comparisons. Nevertheless, dromaeosaurid specimens collected by the Mongolian Academy of Sciences–American Museum of Natural History Expeditions provide an important sample for detailed comparisons with basal avialans and taxa like *Deinonychus antirrhopus*. From the available material, it is apparent that dromaeosaurids and other maniraptorans present a much greater degree of character variation than previously suspected. Below we discuss several areas of the postcranial skeleton in comparison to previously described material.

### STERNUM

Articulation of three or more pairs of ossified sternal ribs with the sternal plates has been described previously among theropods only in an oviraptorid from Ukhaa Tolgod (Clark et al., 1999) and in avialans. The ventral ribs in oviraptorids attach to the sternal plates at their mediolateral constriction between the anterior and posterior lateral processes. The sternal ribs are thin with expanded ends where they attach to the sternal

plates. As described above, although poorly preserved, a small bundle of three ossified sternal ribs is preserved on the left side of IGM 100/976. None of the specimens preserves the lateral margin of the sternum, which would indicate the presence of articular facets for these elements. In Aves, the minimum number of ventral ribs is two, while most have many more—up to nine in swans (Fürbringer, 1888; Clark et al., 1999).

It is apparent that some theropods, including nonmaniraptorans, had attachments between ventral ribs and sternal elements. For instance, a well-preserved sternum of the holotype of *Gorgosaurus libratus* clearly shows attachment facets for two pairs of sternal ribs (Lambe, 1917). The paucity of preserved sternal elements in other derived theropods hampers further understanding of the distribution of this feature. Nevertheless, the presence of three pairs of ossified sternal ribs that articulate with an ossified sternum is a putative synapomorphy within Theropoda for a group minimally containing oviraptorids, dromaeosaurids, and Avialae. These elements are not observed in the most basal avialans because of the fragmentary nature of these specimens with the notable exception of *Confuciusornis sanctus*, which displays



Fig. 19. Pubis of IGM 100/985 in posterior view. Labels are spelled out in appendix 2.

five pairs of sternal ribs (Chiappe et al., 1999).

#### UNCINATE PROCESSES

Free uncinat e processes have been described in *Velociraptor mongoliensis* (Paul, 1988), and confirmed by our own observations on the "Fighting Dinosaurs" specimen in Ulaanbaatar (see Jerzykiewicz et al., 1993: fig 11; and Psihoyos and Knoebber, 1994: 209). Definitive uncinat e processes have not been recovered in any of the specimens of *Velociraptor mongoliensis* collected during the AMNH-MAS expeditions. However, only one specimen (IGM 100/982) preserves this region of the body, which is in extremely poor condition. Some of the broken rodlike elements found disarticulated in the chest region may represent uncinat e processes (fig. 2). Among nonavian theropods, uncinat e processes are otherwise known to occur in oviraptorids (Clark et al., 1999). Because of their sporadic distribution, uncinat e processes may be a synapomorphy for a clade of theropods including birds, or, owing to their putative absence in alvarezsaurids and *Archaeopteryx lithographica*, may represent convergence.

#### FURCULA

The furcula of nonavian theropods differs from that of avialans both in the interclavicular angle and the overall form of the furcula (i.e., V-shaped vs. U-shaped). The furcula of *Archaeopteryx lithographica* is more acute and U-shaped than the furcula of dromaeosaurids, and appears intermediate between the furculae of nonavian theropods and higher Avialae. Within Avialae, however, much variation exists in attributes such as relative size, curvature and cross-sectional profile of the rami, and shape and size of the hypocleidium (fig. 25; Martin et al., 1998).

In an extensive analysis of both fossil birds and other "reptiles" (including dinosaurs), Heilmann (1926) noticed extensive similarities between *Archaeopteryx lithographica* and dinosaurs, specifically the "coelurosaurs." He wrote: "the striking points of similarity between Coelurosaurs and birds pertained to nearly all the parts of the skeleton" and that "from this it would seem a

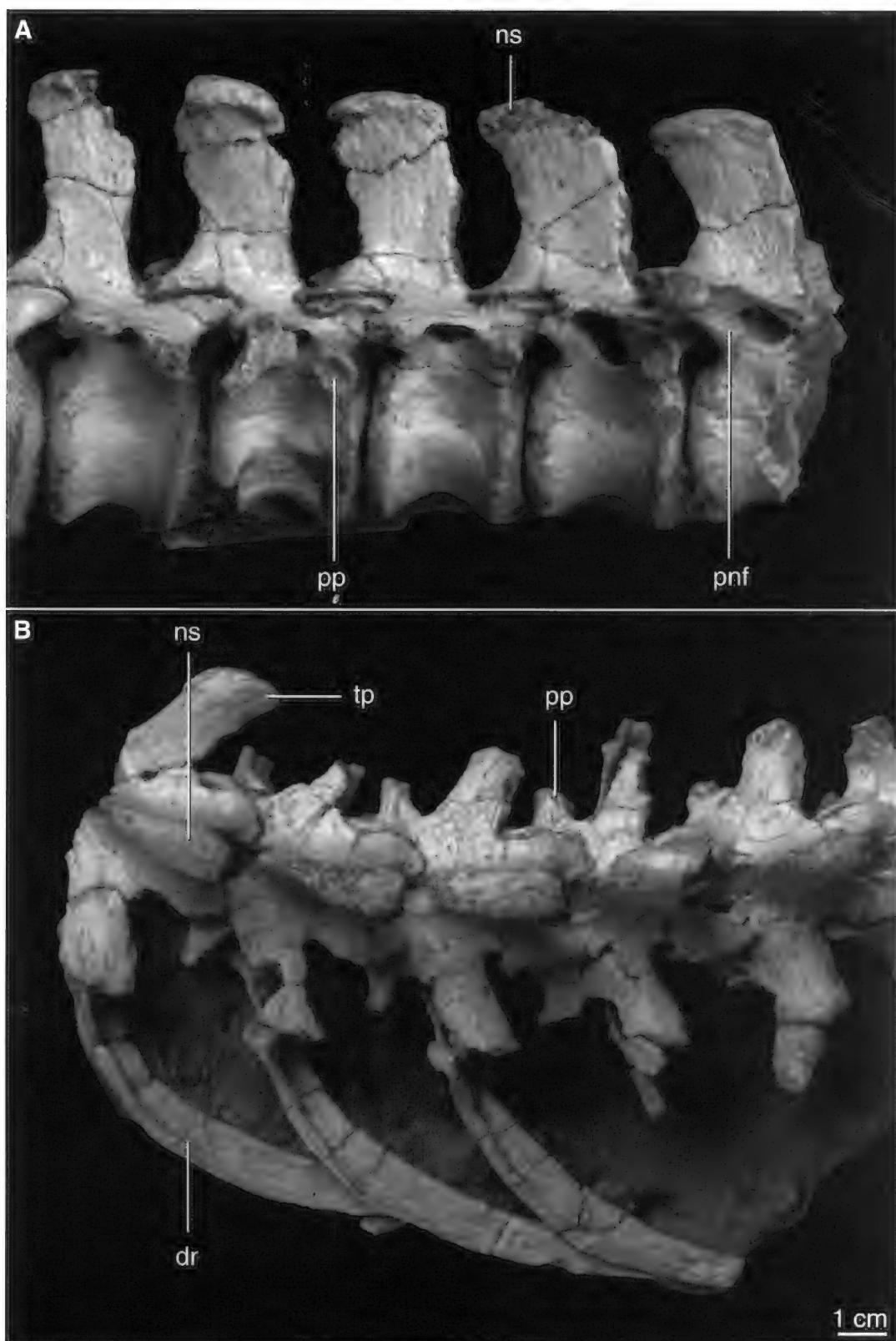


Fig. 20. Posterior dorsal vertebrae of IGM 100/986. A, right lateral; B, dorsal views. Labels are spelled out in appendix 2.



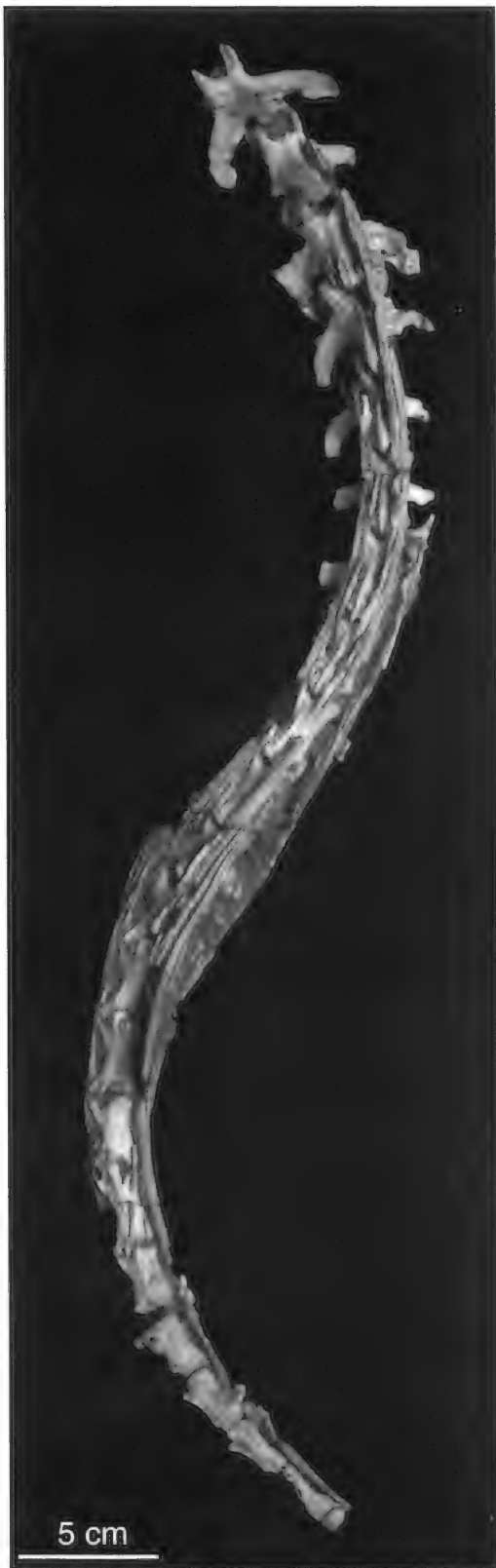


Fig. 21. Tail of IGM 100/986 in dorsal view.

rather obvious conclusion that it is amongst the Coelurosaurs that we are to look for the bird-ancestor" and "We have therefore reasons to hope that in a group of reptiles closely akin to the Coelurosaurs we shall be able to find an animal wholly without the shortcomings here indicated for a bird ancestor." It should be pointed out that Heilmann's definition of coelurosaurs was inexact and can only be compared to Gauthier's Coelurosauria (Gauthier, 1986) generically.

Heilmann's statements were particularly astute, considering the paucity of coelurosaurian specimens available to him. Nevertheless, it is often pointed out that Heilmann tempered his words concerning coelurosaur origins, stating that "And yet, this would be too rash, for the very fact that the clavicles are wanting would in itself be sufficient to prove that these saurians could not possibly be the ancestors of birds." (p. 183). Since Heilmann's work, extensive evidence has documented the presence of a furcula in a variety of theropod taxa (Barsbold, 1976, 1983; Chure and Madsen, 1996; Norell et al., 1997; Makovicky and Currie, 1998). Some of these specimens show this element in articulation (Barsbold, 1976; Norell et al., 1997; Dal Sasso and Signore, 1998). Nevertheless, recalcitrance to this evidence exists.

Notably, Feduccia and Martin (1998) have argued that these elements are not homologous and rather represent some other element, such as gastralia or interclavicles (Feduccia, 1996; Feduccia and Martin, 1998). They have also argued that the furculae of nonavian dinosaurs are dissimilar to that of *Archaeopteryx lithographica*, and that the articulation of the furcula with the shoulder apparatus in *Velociraptor mongoliensis* is dissimilar to that of Aves. Furthermore, because the furcula is intimately involved in the flight apparatus of Aves, Feduccia and Martin argued that it cannot possibly be homologous with that in nonavian dinosaurs because these animals did not fly. Amazingly, it has even been suggested that the furcula among members of Avialae is not a homologous structure and that *Archaeopteryx lithographica* and Aves are descended from a common ancestor that lacked a furcula (Martin et al., 1998)!

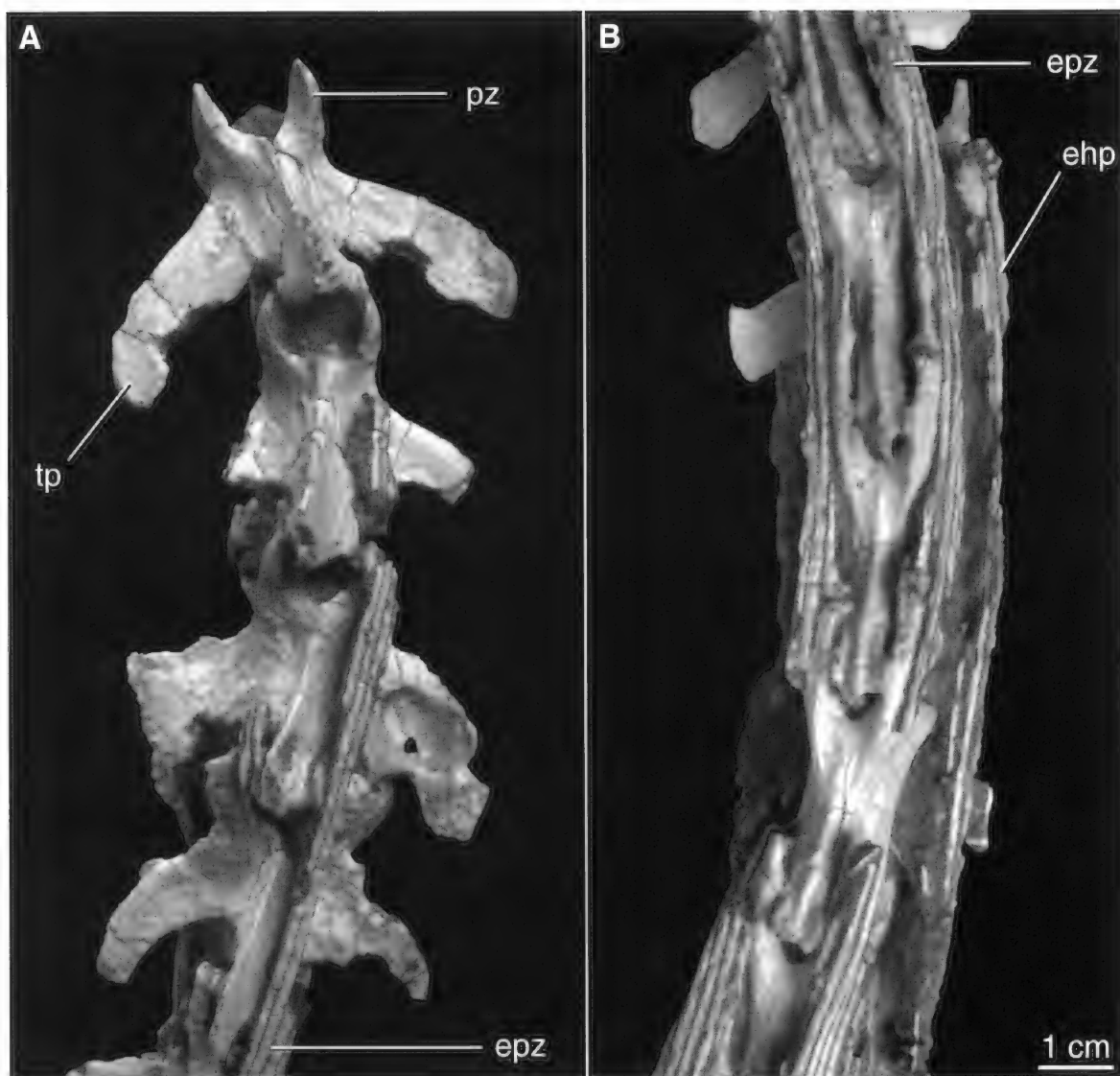


Fig. 22. Tail of IGM 100/986. Dorsal view of details. **A**, anterior section; **B**, midpoint section. Labels are spelled out in appendix 2.

There is much to be said in response to this view (see Norell et al., 1998), but we will limit our comments to a few observations: (1) An interclavicle is unknown in any ornithodiran (Sereno, 1991), and the interclavicle is not involved in the formation of the quail furcula (Russell and Joffe, 1985). (2) The range of variation in furculae in modern birds is striking (fig. 23), which diminishes the significance of differences observed between *Velociraptor mongoliensis* and primitive avialans like *Archaeopteryx lithographica* and *Confuciusornis sanctus*.

(3) The articulation of the furcula with the scapulocoracoid in nonavian dinosaurs is topologically the same as in Avialae. Without examination of the relevant specimens, Feduccia and Martin (1998: 754) claimed that "the articulation of the arms of the *Velociraptor's* furcula-like structure along the entire margin of the coracoid is unlike the articular relationship of the furcula in birds."

In Aves, the furcula articulates with the acromion process of the scapula, however there may be some contact with the acrocoracoid process of the coracoid to form the

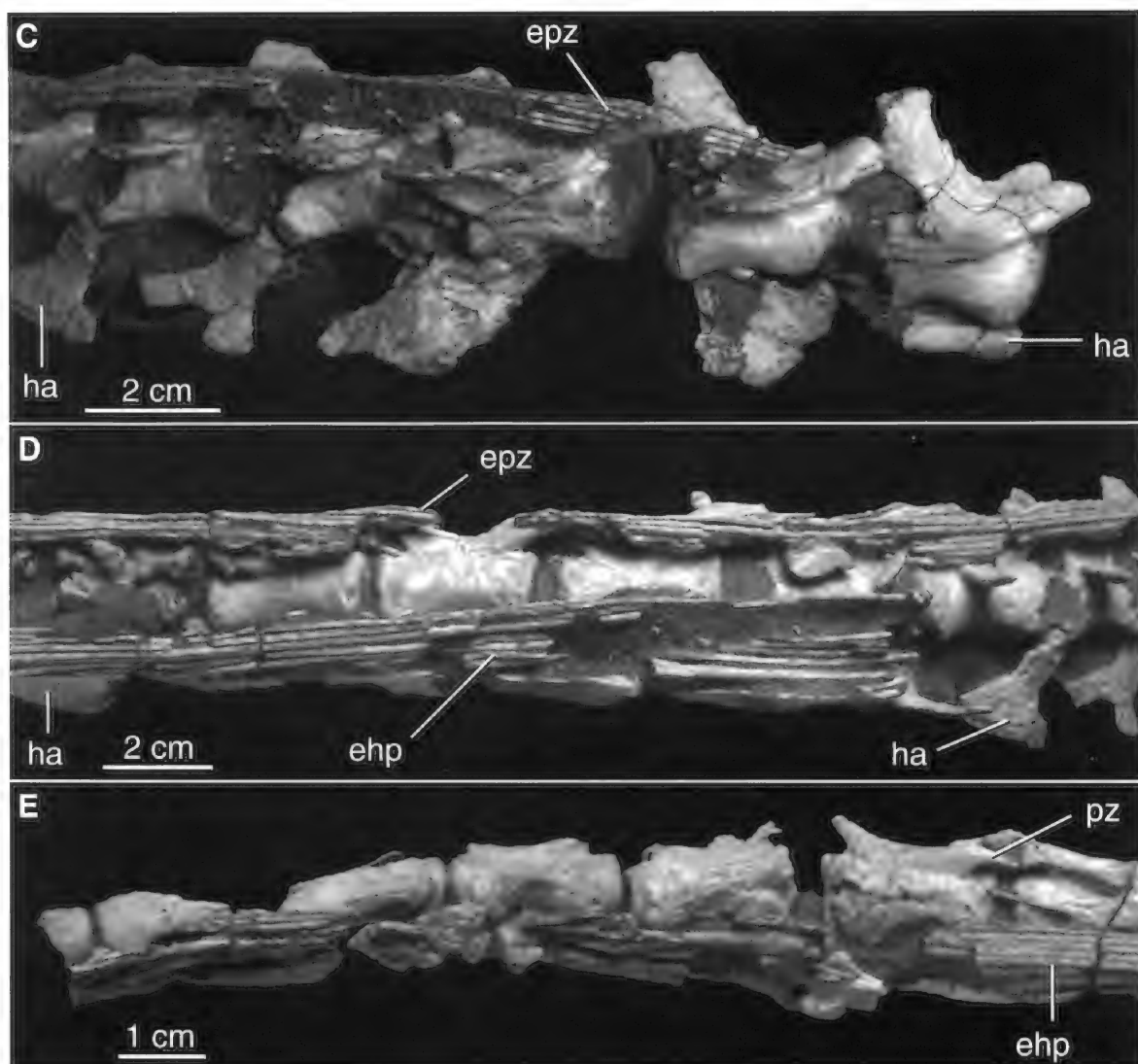


Fig. 22. *continued*. Tail of IGM 100/986. Right lateral view of details. C, anterior section; D, midpoint section; E, posterior section. Labels are spelled out in appendix 2.

triosseal canal (a feature not found in primitive Avialae and nonavian theropoda). Jenkins (1993) has argued that in *Archaeopteryx lithographica*, this articular relationship is the same. However, see Ostrom (1976c: 12) for a cautionary note: "This cannot be established on the basis of the present specimens." This view contrasts to that of Martin (1991, 1995) who suggested that the furcula of *Archaeopteryx lithographica* articulated exclusively with the coracoid tuber, which, if true, would be a unique condition.

The orientation of the furcula and its articulation with the shoulder apparatus is dis-

torted due to collapse of the thoracic cavity in both IGM 100/976 and IGM 100/982. Nevertheless, it is not possible for the furcula to have articulated with the coracoid along its "entire margin" (Feduccia and Martin, 1998). This is because in life the medial margins of the coracoids were in articulation with the sternal elements ventrally or lay in close apposition along the midline. Furthermore, the posteriorly flattened terminal lateral process of the furcula and its relation to the coracoid (shown in IGM 100/976, fig. 3) strongly support the reconstruction of the furcula's position in *Velociraptor mongoliensis*.

TABLE 5  
Measurements for Selected Vertebral Characters in *Velociraptor mongoliensis* (in millimeters)

	Maximum length of centrum				Maximum width across transverse processes			
	IGM 100/976	IGM 100/980	IGM 100/985	IGM 100/986	IGM 100/976	IGM 100/980	IGM 100/985	IGM 100/986
Cervicals								
7	23.6							
8	20.3+							
9	26.3							
Dorsals								
1				27 <sup>a</sup>				
2				24.6				
3	15.2							
8					50.2			44.4
9				18.6	53 <sup>a</sup>			>36.8
10				18.4	53.2			39.9
11				18.4	56 <sup>a</sup>			42.3
12		>12.7	18 <sup>a</sup>	17.8	57 <sup>a</sup>			40.1
13		15.1	16.6 <sup>a</sup>	16.8				38.0
Sacrals								
1		16.5 <sup>a</sup>	17.5	19.5 <sup>a</sup>				
2			17.3	20.1				
3			18.4 <sup>a</sup>	19.5				
4			18.1 <sup>a</sup>	22.6				
5			16.6 <sup>a</sup>	21.2				
6			16.9	20.4				
Caudals								
1			17.0	16.4				>44.1
2		19 <sup>a</sup>	19.1	19.2				>44.5
3		>21.8	20.3	20.8		62.1	49.4	55.1
4		22.8	23.4 <sup>a</sup>	24.1		>59.2	48.9	57.8
5		25.2 <sup>a</sup>	24.5 <sup>a</sup>	24.6		72.7	45.7	55.7
6			24.1	24.8 <sup>a</sup>			42.4	>32.8
7			23.9 <sup>a,b</sup>	23.9				>45.8
8			25.9 <sup>a,b</sup>	25.1				>39.6
9				27.3				>36.9
10				28				>34.5
11				>23.6				36 <sup>a</sup>
12				27.5				
13				26.7				
14				25.4 <sup>a</sup>				
15								
16								
17				26.1				
18				25.7				
19				25.2				
20				24.9				
21				20.7				
22				21.3				
23				22.0				
24				21.2				
25				20.5				

<sup>a</sup> Estimated values.  
<sup>b</sup> Modification from Norell and Makovicky.



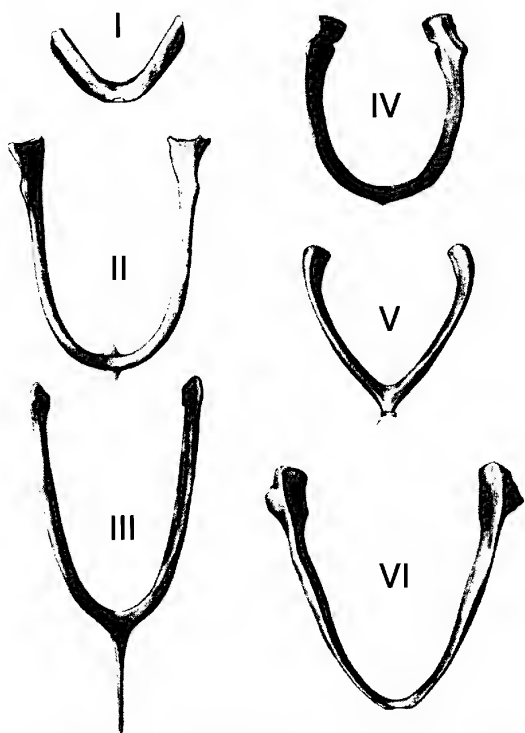


Fig. 23. Some of the extensive variation among furculae in representative Avialae. I *Archaeopteryx lithographica*, II *Corvus corax*, III *Falco peregrinus*, IV *Nyctea nivea*, V *Ciconia argala*, VI *Crax alector*. Modified from Owen, 1863.

sis as contacting the acromion. Specifically, IGM 100/976 shows the furcula displaced anterodorsally, with its ends (especially the right) almost in contact with the acromia, suggesting that the furcula connected to the acromion via a ligament as in Aves and presumably in more primitive theropods (Makovicky and Currie, 1998). This is also borne out by the orientation and articulations of the furcula in several well-preserved specimens of other nonavian theropods, such as oviraptorids (Clark et al., 1999).

Finally, the argument that these bones cannot be furculae because dinosaurs don't fly is a spurious one. As pointed out by several authors (see de Pinna, 1991), the determination of homology comes through the congruence between characters. Functional aspects of structure, whether observable or assumed, are not critical to the establishment of characters that are similar (i.e., primary

homology), and represent a secondary level of inference (Lauder, 1995).

#### PELVIS

In a paper discussing the lung mechanics of theropod dinosaurs, Ruben et al. (1997) suggested that in Avialae the "marked dorsal position and the projection of the distal pubis posterior to the ilium and ischia are associated with suprapubic muscular rotation of the pelvis and tail. Such movements facilitate ventilation of non-vascular air sacs during arboreal roosting. This condition of the pubis is broadly inconsistent with the morphology of the theropod pelvis as well as with hepatic-piston diaphragmatic breathing." (p. 1269).

The functional scenario presented by Ruben et al. (1997) is clearly assumption-laden, and here we comment on their evidence for the reconstruction of the pelvis in *Archaeopteryx lithographica* and corresponding structures in nonavian dinosaurs, specifically *Velociraptor mongoliensis*.

In an earlier paper (Norell and Makovicky, 1997), we described a well-preserved, articulated pelvis of a dromaeosaurid that displayed conclusive evidence of opisthopuby in dromaeosaurids. Furthermore, the posterior extension of the pubis in our specimens (IGM 100/982, 100/985, and 100/986) is longer than the ischia and the postacetabular ilia (Norell and Makovicky, 1997: fig. 12), as is also true of an undescribed dromaeosaurid from Khulson (IGM 100/980) (fig. 24). Several authors have commented on the presence of a hypopubic cup formed on the posterior (or, in the case of extreme opisthopuby, posterodorsal) surface of the pubis at the symphysis (Tarsitano and Hecht, 1980; Martin, 1991; Ruben et al., 1997). This structure is putatively observable in only two specimens of *Archaeopteryx lithographica*, those in London and Eichstätt. In the Eichstätt specimen the structure is incomplete and appears only as a flattened area on the distal extremity of the pubes as reconstructed by Martin (1991: fig. 33). This reconstruction cannot be reconciled with the specimen, where the distal pubes actually are preserved in lateral view and there is no obvious indication of a cup or distally flattened area. In the London



Fig. 24. Undescribed dromaeosaurid from Khulson (IGM 100/980), showing the extreme length of the pubis and an opisthopubic condition. Labels are spelled out in appendix 2.

specimen the purported hypopubic cup consists of an irregular mass of calcite that is discontinuous with the darker periosteal bone of the pubic shafts (fig. 25) and interpreted as cartilaginous (De Beer, 1954: 27). The visible ends of the pubic shafts appear to form a narrower symphysis than the calcitic mass that partially covers them. The posterior excavation is an artifact. Although this mass glows under ultraviolet light (De Beer, 1954), it has a rough crystalline composition unlike other bony elements on the two slabs. If this mass represents remnants of some cartilaginous mass (as interpreted by De Beer [1954]) associated with the distal ends of the pubes, it is not comparable to other theropods where such soft tissue structures are not preserved. As described above, the pubes of both IGM 100/986 and 100/985 display a slight transverse expansion distally, however the extent of the "cup" structure is also difficult to determine.

We suggest that the presence of a hypopubic cup in *Archaeopteryx lithographica* is still conjectural and that the character of interest is the plesiomorphic transverse expan-

sion of the pubic symphysis just distal to the pubic apron—a character shared by *Archaeopteryx lithographica*, *Velociraptor mongoliensis*, and many more primitive theropods.

A second issue concerns Ruben et al.'s reconstruction of the pubis in *Archaeopteryx lithographica*, which they reconstruct in the most extreme opisthopubic position yet presented—even more so than that proposed by Martin (1995: fig. 2), which requires a constricted elliptical acetabulum. They claimed that "The position of the pubis in *Archaeopteryx lithographica* has occasionally been interpreted as having been vertical rather than severely opisthopubic. However, the overall similarity of the pelvis of *Archaeopteryx lithographica* to those of the enantiornithine birds, especially in the presence of the hypopubic cup, as well as the morphology of the London and Berlin *Archaeopteryx lithographica* specimens, offer support for our interpretation of the pelvic structure of these early birds." (Ruben et al., 1997: 1270).

This reconstruction is at odds with other published reconstructions of these pelves

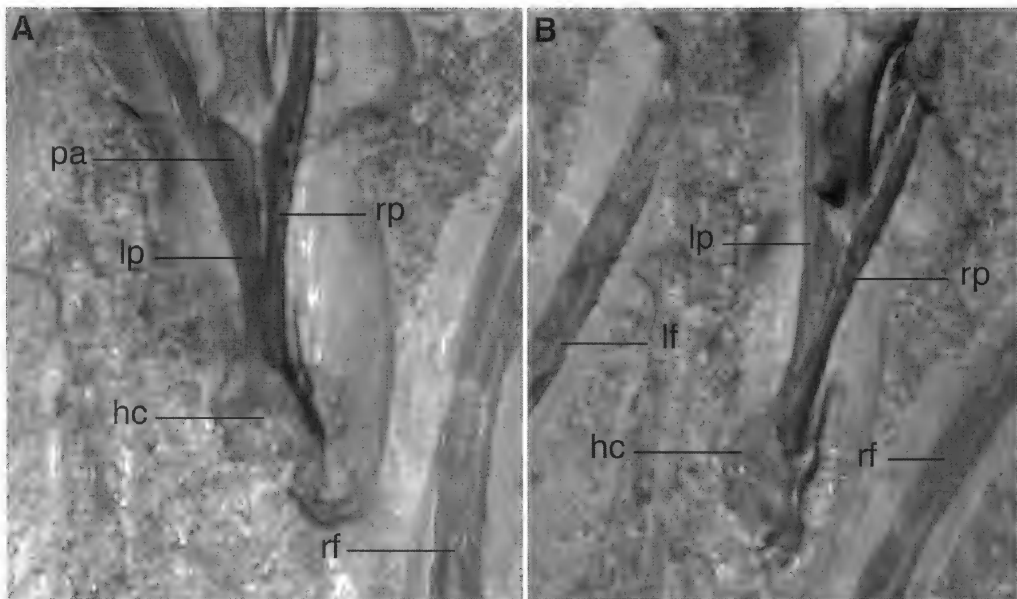


Fig. 25. Distal ends of the pubes of the London specimen of *Archaeopteryx lithographica* in (A) dorsal and (B) right dorsolateral views. The calcitic mass interpreted to be either cartilage or a hypopubic cup is seen to be distinct from the bone of the pubic shafts. See appendix 2 for abbreviations.

(Ostrom, 1976a; Wellnhofer, 1993). Unfortunately, supporting evidence for their conclusions is not presented. From our own observations of these specimens and reviews of the literature, illustrations, and photographs, their conclusions cannot be unambiguously supported. In three of the five specimens of *Archaeopteryx lithographica* that preserve a pubis, including the seventh that displays an unbroken and undistorted pelvis (Wellnhofer, 1993), this element is preserved in a slightly opisthopubic to subvertical orientation. In the other two specimens (Berlin and London), a fracture is evident at the proximal end of the pubis (Berlin) or the pubis is disarticulated (London). *Rahonavis ostromi*, a probable sister taxon to *Archaeopteryx lithographica* (Forster et al., 1998), displays a subvertical orientation, as does the basal alvarezsaurid *Patagonykus puertai* (Novas, 1996). A similar condition is present in the maniraptoran *Unenlagia comahuensis* (Novas and Puerta, 1997).

Many arguments concerning the physiology of maniraptoran dinosaurs, the origin of flight, and the origin of birds have hinged on reconstruction of the pelvis. For instance, the retroverted pubis was cited as evidence for arboreality in avialans (Ruben et al., 1997;

Martin, 1995) or dromaeosaurids and avialans (Chatterjee, 1997; Nesson, 1995). However, as pointed out above, these reconstructions are not in accord with the available evidence in that they place the pubis in too drastic a posterior position. Ironically, the dromaeosaurid pelvis (which shares many morphological similarities with the pelvis of *Archaeopteryx lithographica*) is as extreme as the most opisthopubic reconstructions suggested for *Archaeopteryx lithographica*.

#### FOURTH TROCHANTER

On IGM 100/986 (fig. 10) and IGM 100/982 a large fourth trochanter is present on the femur. This trochanter is a common feature in primitive theropods (Gauthier, 1986) but is also present in a variety of avialans, including *Mononykus olecranus*, although it is absent in *Archaeopteryx lithographica* (Chiappe et al., 1996). Interestingly, this feature is lacking in *Deinonychus antirrhopus* (Ostrom, 1976b), as well as in an unnamed dromaeosaurid (IGM 100/981) from Khul-

The fourth trochanter is generally regarded as the insertion area for the caudofemoralis, and its reduction and loss in maniraptorans

has broad implications regarding locomotion and gait. Its presumed absence in a variety of coelurosaurian taxa has led Gatesy to propose that the caudifemoral leg retraction system of these animals was reduced and that they displayed a kind of "incipient knee based limb retraction" (Gatesy, 1995: 230). The presence of a fourth trochanter in at least one dromaeosaurid taxon (*Velociraptor mongoliensis*) and its absence in others somewhat complicates this proposal.

#### VERTEBRAE

The shape of the dorsal vertebrae varies among coelurosaurian theropods. The trunk vertebrae of ornithomimids and *Coelurus* have axially elongate, spool-shaped centra, which form a tall oval in cross section. Those of dromaeosaurids, oviraptorids, and troodontids are proportionately shorter, wider, and more circular in cross section. The pronounced foreshortening in dorsal centrum length has been suggested as a deinonychosaurian synapomorphy (Serenó, 1997), as has possession of large hypapophyses (Gauthier, 1986) and distally expanded neural spines (Makovicky and Sues, 1998). The vertebrae of *Archaeopteryx lithographica* are difficult to evaluate because of crushing and articulation, but the dorsal vertebrae of *Rahonavis ostromi* resemble those of more derived maniraptorans. Alvarezsaurids have unique, highly derived dorsal vertebrae, with deep keels and opisthoceolous or biconvex articulations.

Although Gauthier (1986) cited the presence of enlarged hypapophyses as a diagnostic feature of maniraptoran theropods, there has been some confusion regarding this character because it has not been adequately described for most relevant taxa. The anterior dorsal vertebrae of some specimens of *Velociraptor* bear a robust, ventrally rounded hypapophysis (IGM 100/976, 100/986), but some variation is evident in the size and shape of these processes. In specimens referred to the velociraptorine *Sauromitholestes langstoni*, the hypapophyses are proportionately longer and more blade-like than in *Velociraptor mongoliensis*. The hypapophysis is broken in an anterior dorsal vertebra of *Deinonychus antirrhopus* (YPM 5210), but the base suggests it may have been large. A

smaller hypapophysis is present on a second, more posterior dorsal vertebra (YPM 5204). Large hypapophyses are also present in troodontids, oviraptorosaurs, and *Ornitholestes hermanni* as well as in many taxa within Aves. In basal avialans, hypapophyses remain undescribed for *Archaeopteryx lithographica* and enantiornithine birds, but are known from *Rahonavis ostromi* (Forster et al., 1998), hesperornithiforms, and *Ichthyornis* (Marsh, 1880). A small structure near the anterior end of the tenth presacral of the Berlin specimen of *Archaeopteryx lithographica* may represent a hypapophysis (personal obs.), but this needs to be verified.

Velociraptorine dromaeosaurids are characterized by having stalked parapophyses on the dorsal vertebrae, where the articular facet for the tuberculum projects laterally from the neural arch pedicel. This derived character is known elsewhere among maniraptorans only in *Unenlagia comahuensis* and in the vertebrae of the alvarezsaurids *Mononykus olecranus* and *Shuvuuia deserti*. It has not yet been reported in *Archaeopteryx lithographica* or *Rahonavis ostromi*, although preservation may preclude establishment of the presence or absence of this derived character in these basal avialans.

#### COMMENTS ON *UNENLAGIA COMAHUENSIS*

Novas and Puerta (1997) described the unusual theropod *Unenlagia comahuensis* from Upper Cretaceous strata in Patagonia. Although extremely fragmentary, this specimen appears to have a number of derived characters that prompted Novas and Puerta (1997) to place it in a sister-group relationship to Avialae, exclusive of other nonavian Theropoda. Some of the features shared by *Unenlagia comahuensis* and avialans are also present in *Velociraptor mongoliensis*, however. These include derived characters of the pelvis, the dorsal vertebrae, and the shoulder girdle.

A concave surface formed on the dorsal surface of the pubic symphysis (see above discussion) is present in *Archaeopteryx lithographica* and *Unenlagia comahuensis*. Ruben et al. (1997) suggested its presence in enantiornithines; however, they did not refer any specimens. The well-preserved enantiornithine



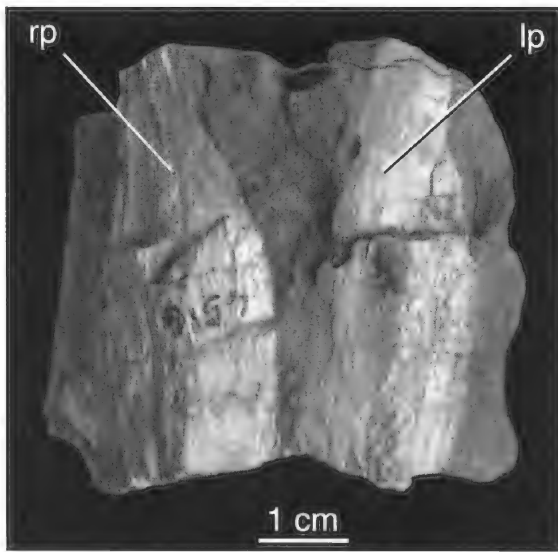


Fig. 26. Holotype pubes of *Saurornithoides mongoliensis* (AMNH 6516) in anterior view, showing development of a pubic apron. Labels are spelled out in appendix 2.

nithine *Concornis lacustris* (Sanz et al., 1995) and the non-enantiornithine *Confuciusornis sanctus* (Chiappe et al., 1999) clearly lack this structure, although they do display a pubic symphysis. Furthermore, the pelves of both *Unenlagia comahuensis* and *Archaeopteryx lithographica* share with dromaeosaurids the presence of a pubic apron formed by pubes that expand distally to form a concave dorsal surface proximal to the boot. Although oviraptorids are not opisthopubic, a similar doubly concave surface, or pubic apron, has been reported for a large specimen from Ukhaa Tolgod (Clark et al., 1999), but such a morphology is absent in IGM 100/50 and 100/30. As is apparent from *Saurornithoides mongoliensis* (AMNH 6515), a dorsally concave pubic apron is also present in troodontids (fig. 26). Additionally, in *Unenlagia comahuensis* and dromaeosaurids, the proximomedial corner of each side of the pubic apron is deflected posteriorly, forming a characteristic small point on the midline of the proximal end of the pubic apron.

The ilium of IGM 100/985 bears a small cuppedicus fossa on the antiliac shelf (Norell and Makovicky, 1997) that wraps onto an expanded pubic peduncle. IGM 100/986 and 100/982 show identical conditions. A com-

parable morphology is present in *Archaeopteryx lithographica*. The reported cuppedicus fossa on the antiliac shelf of *Unenlagia comahuensis* may be an artifact, because the right ilium of the specimen shows a clear fracture and displacement of the ventral preacetabular margin in this region. The left ilium is more similar to that of *Velociraptor mongoliensis* and *Archaeopteryx lithographica* in that it has a laterally deflected ventral margin on the antilium and an expansion of this area onto the pubic peduncle.

A noteworthy detail of the anatomy of *Unenlagia comahuensis* is the lateral, rather than posteroventral, orientation of the glenoid fossa, which is apparently similar to that of basal avialans (Novas and Puerta, 1997). This is considered to have allowed *Unenlagia comahuensis* to undertake "extensive forelimb elevation," indicating "that the forelimbs were capable of excursions in the avian manner" (Novas and Puerta, 1997: 391).

In addition to the repositioning of the glenoid, a modification in the overall orientation of the scapulacoracoid is necessary to achieve avialan humeral motility. Unfortunately, elements that show this were not preserved in the holotype of *Unenlagia comahuensis*. *Velociraptor mongoliensis* displays a glenoid fossa oriented similar to, but not as extreme as, that in *Unenlagia comahuensis*. Furthermore, other pectoral girdle characters that generate a more horizontal and more dorsal position of the scapula are present in *Velociraptor mongoliensis* (see below). A further putative synapomorphy shared by *Velociraptor mongoliensis* and *Unenlagia comahuensis* is the pronounced curvature of the scapula close to the glenoid. In more primitive theropods, this curvature is less pronounced and the scapular blade appears straighter in dorsal view.

The preserved dorsal vertebrae of *Unenlagia comahuensis* share two features with dromaeosaurids that are not present in basal Avialae. Dromaeosaurid dorsal vertebrae are characterized by having "stalked" parapophyses that project laterally from the centrum (Ostrom, 1969a, b), and this condition is also present in *Unenlagia comahuensis*. Another similarity between velociraptorines and *Unenlagia comahuensis* is the mediolateral

expansion of the tip of the neural spine in the posterior dorsal vertebrae, but this condition is also present in troodontids. Similarly, *Unenlagia comahuensis* and some velociraptorines (*Deinonychus antirrhopus* and *Saurornitholestes langstoni*) share the presence of pneumatic foramina in the centra of the thoracic vertebrae (also seen in *Rahonavis ostromi*, but not *Archaeopteryx lithographica*).

*Unenlagia comahuensis* is an interesting animal and further comment on its morphology and phylogenetic relationships awaits more complete anatomical description. Nevertheless, its status as a phylogenetically intermediate link between nonavian dinosaurs and avialans needs to be examined within a larger phylogenetic context, one that includes *Velociraptor mongoliensis* and related taxa.

## CONCLUSIONS

The evidence presented here and in a previous paper clears up several common misconceptions regarding aspects of dromaeosaurid anatomy that are relevant to understanding the origin of Avialae. For instance, the pelvis of nonavian dinosaurs has been portrayed as different from that in basal Avialae. Ruben et al. (1997: 1270) remarked that "A few theropod dinosaurs possess a moderately opisthopubic pelvis, but the distal pubis remains ventrally situated and the degree of dorsal rotation of the pubis does not approximate that in *Archaeopteryx* and the enantiornithine birds." As discussed above, except for minor details of proportion and the orientation of the pubis, the pelvis of *Velociraptor mongoliensis* is exceedingly similar to that of *Archaeopteryx lithographica*.

The pectoral girdle of *Velociraptor mongoliensis* shares several derived characters with that of *Archaeopteryx lithographica*. These include the large and curved coracoids that face anteriorly, as evidenced by their articulation with the anterior surface of the sternum. This arrangement brings the glenoid into a lateral orientation relative to the condition in theropods with smaller coracoids and sterna, and is enhanced by the reorientation of the glenoid on the scapulacoracoid. Martin (1991) illustrated the pectoral girdle

of *Archaeopteryx lithographica* with the coracoids lying far apart and the furcula articulating to the coracoid tubercle (= biceps tubercle). Such a configuration, if real, would be unique among amniotes, and is not supported by articulated dinosaur skeletons with the clavicles or furculae in articulation (Russell and Dong, 1993; Norell et al., 1997; Brown and Schlaikjer, 1940). A more reasonable reconstruction is given in Wellnhofer (1993) where the coracoids are almost in contact, abutting the dorsolateral margins of the sternum. Wellnhofer's reconstruction also shows the expanded posterior margin of the coracoid with the large triangular subglenoid fossa ventrolateral to the glenoid on the coracoid and the flexure of the coracoid giving the entire scapulacoracoid an L-shape (see also Tarsitano and Hecht, 1980: fig. 2). Many of these features were also noted by Ostrom (1976a: fig. 13), in *Deinonychus antirrhopus*.

In summary, the pectoral girdle of *Velociraptor mongoliensis* displayed in the specimens reported here requires revision of Martin's (1995: 36) statement that "Dinosaurs also have long narrow scapulae but they cross the rib cage on the lateral side while in birds, including *Archaeopteryx lithographica*, the scapula lies on the back." Instead, at least in dromaeosaurids, the scapulacoracoid is held firmly against the sternum, in a way that fixes the orientation of the scapula and the glenoid. Instead of being situated at a low angle along the side of the trunk, the scapulae lay in a subhorizontal position, and high on the back adjacent to the vertebral column (fig. 27).

Although the pectoral girdle changes dramatically in more advanced avialans (i.e., the coracoid loses its L or hook-shape and becomes strutlike), the similarity between the pectoral apparatus of *Archaeopteryx lithographica* and *Velociraptor mongoliensis* and the fragmentary remains of *Unenlagia comahuensis* suggests that similar ranges of motion were present in all three animals. This mobility—combined with the presence of a folding mechanism in the wrist distally as a primitive character for maniraptorans—indicates that these features originated phylogenetically before the origin of powered flight in avialans.



Fig. 27. A, IGM 100/982 in right lateral view; B, detail showing subhorizontal position of scapula high on rib cage and adjacent to vertebral column. Labels are spelled out in appendix 2.

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APPENDIX 1

Because some confusion exists regarding published specimen numbers of theropods from the MAS-AMNH expeditions, the following annotated table lists all specimens published up to this time.

IGM #	Year collected	Taxon	Material	Locality	Citations	Comments
100/99	1991	<i>Shuvuuia deserti</i>	partial skeleton	Tugrugeen Shireh	Chiappe et al., 1996	referred to <i>Mononykus olecranus</i> in Chiappe et al., 1996; later referred to <i>Shuvuuia deserti</i> in Chiappe et al., 1998
100/971	1993	oviraptorid	embryo	Ukhaa Tolgod	Norell et al., 1994; Norell and Clark, 1997	
100/972	1993	troodontid	skull	Ukhaa Tolgod	Norell et al., 1994	these specimens were referred to the Dromaeosauridae in Norell et al., 1994; Norell et al., submitted, show that they are actually troodontids
100/973	1993	oviraptorid	skull and skeleton	Ukhaa Tolgod	Novacek et al., 1994	
100/974	1993	troodontid	skull	Ukhaa Tolgod	Norell et al., 1994	these specimens were referred to the Dromaeosauridae in Norell et al., 1994; Norell et al., submitted, show that they are actually troodontids
100/975	1993	<i>Shuvuuia deserti</i>	partial skeleton	Ukhaa Tolgod	Chiappe et al., 1996	referred to <i>Mononykus olecranus</i> in Chiappe et al., 1996; later referred to <i>Shuvuuia deserti</i> in Chiappe et al., 1998
100/976	1991/1992	<i>Velociraptor mongoliensis</i>	partial skeleton and skull	Tugrugeen Shireh	this paper	
100/977	1994	<i>Shuvuuia deserti</i>	skull and partial skeleton	Ukhaa Tolgod	Chiappe et al., 1996	referred to <i>Mononykus olecranus</i> in Chiappe et al., 1996; later referred to <i>Shuvuuia deserti</i> in Chiappe et al., 1998
100/979	1993	oviraptorid	partial postcranial skeleton on nest	Ukhaa Tolgod	Norell et al., 1995; Clark et al., 1998	in the figure caption of Norell et al., 1995, this specimen is mislabeled as IGM 100/972
100/980	1991	dromaeosaurid	partial skeleton	Khulson	this paper	
100/982	1995	<i>Velociraptor mongoliensis</i>	skull and skeleton	Flaming Cliffs	Norell and Makovicky, 1997; this paper	
100/985	1993	<i>Velociraptor mongoliensis</i>	partial skeleton	Tugrugeen Shireh	Norell and Makovicky, 1997; this paper	called Dromaeosauridae indet. Norell and Makovicky, 1997
100/986	1993	<i>Velociraptor mongoliensis</i>	partial skeleton	Chimney Buttes	Norell and Makovicky, 1997; this paper	
100/987	1993	ornithomimid	braincase and fragmentary postcrania	Ukhaa Tolgod	Makovicky and Norell, 1998	
100/1001	1995	<i>Shuvuuia deserti</i>	skull and partial postcrania	Ukhaa Tolgod	Chiappe et al., 1996	referred to <i>Mononykus olecranus</i> in Chiappe et al., 1996; later referred to <i>Shuvuuia deserti</i> in Chiappe et al., 1998

## APPENDIX 2

## Anatomical abbreviations used in this paper

a	astragalus	lsp	left sternal plate
aa	ascending process of astragalus	lt	left tarsal
ac	acromion	ltr	lesser trochanter
ais	antiliac shelf	lvr	left ventral ribs
ca	calcaneum	mco	medial condyle
cc	cnemial crest	ns	neural spine
cf	coracoid foramen	pa	pubic apron
ct	coracoid tuber	pb	pubic boot
cv	cervical vertebra	pf	popliteal fossa
dr	dorsal rib	pnf	pneumatic foramen
ect	ectocondylar tuber	pp	parapophysis
ehp	anterior extension of neural arch processes	ppd	pubic peduncle
epz	anterior extension of prezygapophysis	pt	posterior trochanter
f	furcula	pz	prezygapophysis
fc	fibular crest	rc	right coracoid
fh	femoral head	rf	right femur
fi	fibula	rh	right humerus
ft	fourth trochanter	ri	right ilium
g	glenoid	ris	right ischium
gt	greater trochanter	rmc	right metacarpal
ha	hemal arch	rmt	right metatarsal
hc	hypopubic cup	rp	right pubis
la	left acromion	rs	right scapula
lc	left coracoid	rscp	right sternal process of coracoid
lco	lateral condyle	rsp	right sternal plate
lf	left femur	rt	right tarsal
li	left ilium	sar	supra-acetabular rim
lis	left ischium	suf	subglenoid fossa
lmt	left metatarsal	t	tibia
lp	left pubis	tlc	lateral condyle of tibia
lr	lateral ridge	tmc	medial condyle of tibia
ls	left scapula	tp	transverse process
lscp	left sternal process of coracoid	vf	venous foramen







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